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# The Nitrogen Budget of Two Salt Desert Shrub Plant Communities of Western Utah

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# THE NITROGEN BUDGET OF TWO SALT DESERT SHRUB PLANT COMMUNITIES OF WESTERN UTAH

by

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Richard S. Bjerregaard

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# ABSTRACT

The Nitrogen Budget of Two Salt Desert Shrub
Plant Communities of Western Utah

by

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The nitrogen budgets of Eurotia lanata (Pursh.) Moq. and Atriplex confertifolia (Torr. and Frem.) S. Wats salt desert shrub plant communities were investigated. In each, a complete biomass and organic nitrogen inventory was made. In addition, investigations of the nitrogen fixation potential of soil surface microflora and inorganic soil nitrogen relationships were carried out.

Greater total biomass and organic nitrogen was found in the above-ground portions, annual shoot productivity, and litter of the Atriplex community. However, the Atriplex community was exceeded by the Eurotia community in root biomass. Roots accounted for 74 and 87 percent of the plant biomass and 83 and 90 percent of the associated organic nitrogen in Eurotia and Atriplex communities respectively. Root biomass distribution at various depths was markedly different in the two communities. Differences between communities in relative amounts of various plant parts and litter

are related to contrasting plant growth habit, and differences in soil texture and soil salinity. Total plant biomass estimates, which were 18,480 and 17,300 kilograms per hectare for Eurotia and Atriplex communities, were not significantly different and reflect the overriding influence of macroclimate and associated moisture limitation.

Under laboratory conditions the soil surface microflora of the Atriplex community was able to fix significant amounts of atmospheric nitrogen while that of the Eurotia community did not. Nitrogen fixation potential in the Atriplex community was associated with the presence of abundant lichen cover and associated heterocyst-containing blue-green algae of lichen interspaces.

Differences between communities were found in rates of mineralization, downward flux, and pattern of utilization of inorganic soil nitrogen. Soil salinity appeared to strongly limit inorganic soil nitrogen mineralization as well as root growth and nitrogen uptake in the lower part of the Atriplex soil profile; however, this lack of biological activity was compensated for by a greater downward flux of inorganic soil nitrogen from decomposing litter and surface soil in the Atriplex community. Shoot and root litter appears to be the most readily available source of inorganic soil nitrogen for plant growth in salt desert shrub plant communities.

(100 pages)

# CHAPTER I

## INTRODUCTION AND DESCRIPTION OF STUDY AREA

Nearly monospecific communities of salt desert shrubs dominate much of the cold desert areas of the Intermountain region. Because of their large areal extent, these communities are important to the ecological well-being of the Intermountain area and have long been the object of ecological investigation. The goal of many of these investigations has been to elucidate the strategies whereby desert plant species grow and survive in very dry and often osmotically unfavorable habitats (Workman and West, 1967; Gasto, 1969). Others have sought to establish the criteria by which these salt desert shrub communities could safely be grazed by domestic livestock (Cook and Stoddart, 1963). However, only recently have ecologists begun to give impetus to the study of primary productivity and plant nutritional relationships at the community level.

Nitrogen is needed in substantial quantities by plants. The fixation of nitrogen into biologically active forms, its accumulation and conservation in organic forms in ecosystems, and the rates of its transformation in each part of the biogeochemical cycle is important to the overall productivity of desert plant communities. Because of the importance of nitrogen in the functioning of desert ecosystems, research was initiated in 1968 to evaluate quantitatively the nitrogen cycle of two ecologically distinct and widely distributed salt desert shrub plant communities of western Utah.

This quantative evaluation included the following objectives: (1) To make a complete plant biomass and nitrogen inventory and estimate the nitrogen accumulated in the above-ground annual productivity in each plant community; (2) To evaluate the collective soil surface microflora from each plant community as a source of biologically fixed nitrogen for higher plants; (3) To investigate inorganic soil nitrogen relationships, including fluxes and concentrations of inorganic soil nitrogen during the course of an annual cycle; (4) To integrate the findings of the investigation into a conceptual model of the nitrogen budget of cold desert ecosystems.

Adjacent and nearly monospecific stands of Atriplex confertifolia and Eurotia lanata, located in Box Elder County, Utah at 1350 meters elevation and about 10 kilometers north of Kelton (Mitchell, 1965), were chosen as study sites. The study sites lie in a broad flat lacustrine valley occupied by Lake Bonneville during the Pleistocene epoch. According to Gilbert (1890), the Lake exerted a major effect upon the soils and topography of the area. The shore lines, as well as other influences of Lake Bonneville, are at the present time almost unmodified.

The soils in the immediate vicinity of the study plots are relatively homogenous. Textures vary somewhat, but usually are of silt loam or sandy loam texture; however, the soil of the Eurotia plot (Figure 1) appeared to have a coarser texture than the soil of the Atriplex plot (Figure 2). Eurotia and Atriplex soils differ significantly in salt content (Figure 3). The Atriplex soil contains substantially greater amounts of soluble salt than the Eurotia soil

at all depths except surface soil (0-2 cm), a factor which has a significant influence upon the rooting habit of the dominant plants. Soil pH of the study plots ranged from 7.82 to 8.51. Variation in soil pH with depth was inconsistent; however, mean pH values were about 8.0. The greatest pH values were observed in the surface soil of the Atriplex community and are probably due to the greater tendency of this plant to accumulate sodium salts in its leaves and stems. Sodium salts, responsible for high pH, are subsequently released to surface soil during litter fall and decomposition.

The biotic communities of this area are considered to be part of the Northern Desert Shrub Biome (Fautin, 1946). This Biome consists of two main plant associations, shadscale and sagebrush. Plant communities range from pure stands to scattered individuals of the dominant shrub species intermixed with various grasses, forbs, and lesser shrubs.

Study plots chosen for this investigation are representative of the shadscale zone and consist of nearly pure stands of Atriplex confertifolia (Torr. and Frem.) S. Wats and Eurotia lanata (Pursh) Moq. (Figures 1 and 2). Of the two, Atriplex confertifolia appears to be the most salt tolerant and is usually found on soils which are finer textured, more xeric, and often laden with various mineral salts. Other dominant shrubs occupying areas of similar climate and soils are Atriplex species, Sarcobatus vermiculatus (Hook.) Torr., Graya spinosa (Hook.) Moq., Kochia americana S. Wats., and Artemisia species. Several annual invading species are common in the study area. These include Halogeton glomeratus (Bieb.) Mey., Bromus tectorum L., and

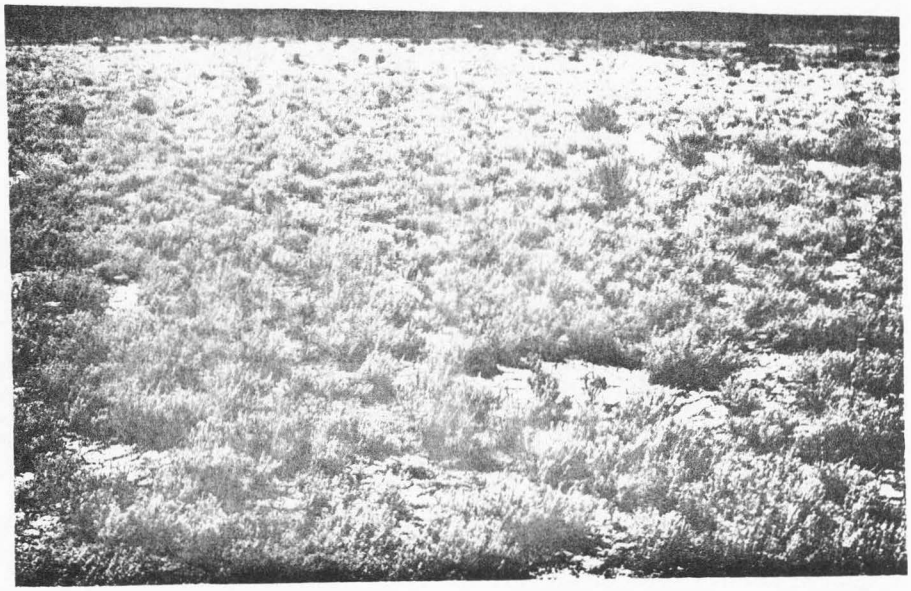


Figure 1. A general view of the Eurotia lanata study area.

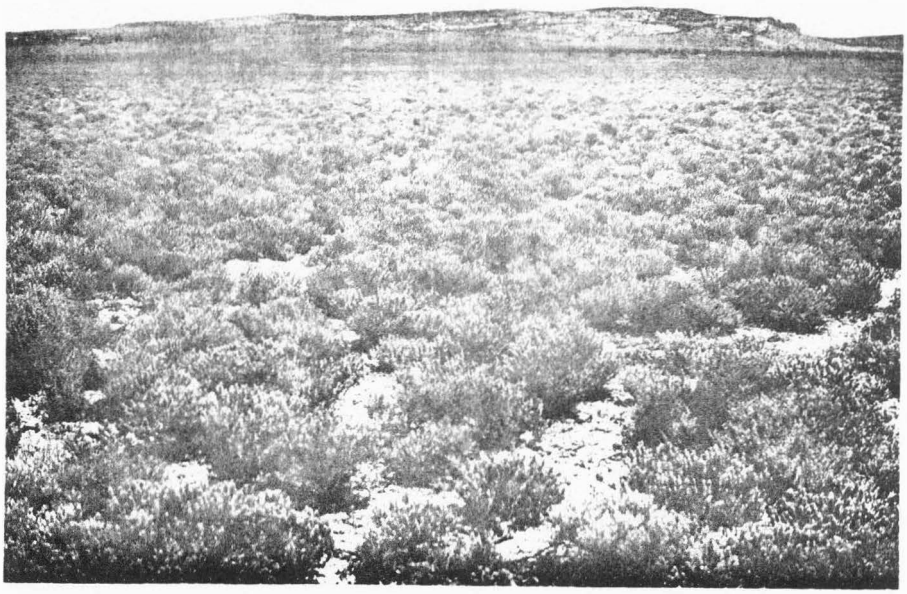


Figure 2. A general view of the Atriplex confertifolia study area.

Salsola kali L., which rapidly cover areas bared by disturbance (nomenclature follows Welsh, Treshow, and Moore, 1964).

The climate of the study sites is semiarid with warm dry summers and cold winters. The harsh climate of the area is well characterized by the annual precipitation of approximately 250 mm. Annual and seasonal precipitation is quite variable as evidenced by precipitation during June, 1967 when 34 percent of the annual total fell (Coyne, 1969). Air temperatures commonly range from below 0 C to above 40 C during the growing season which begins late in March and lasts as long as soil moisture is available from plant growth (Moore, 1971).

# CHAPTER II

# TOTAL NITROGEN INVENTORY

## Introduction

A biogeochemical cycle involves the cyclic transfer of nutrients between atmosphere, water, soil, plant, and animal components of the ecosystem. Each component part of the ecosystem has, associated with its organic matter, a certain proportion of the system's biologically active nutrient capital. Thus a complete biomass inventory is the first essential step in the development of a nutrient budget for a soil-vegetation system. The purpose of this step is even more firmly established by the fact that the rates of biomass turnover and nutrient transformations cannot be effectively integrated without information on nutrient pool size in each compartment of the system.

The salt desert shrub community can be subdivided into four major nitrogen containing organic matter compartments. They are: (1) above-ground portions of plants (shoots), (2) below-ground portions of plants (roots), (3) litter, and (4) soil. These major compartments can be further subdivided on the basis of ecologically significant properties of each. Shoots can be subdivided into new growth (net biomass accumulated during the current growing season) and old growth (net biomass accumulation of past growing seasons), root biomass according to its distribution in the soil profile, and litter biomass according to its type and resistance to decomposition. The soil profile as well must be subdivided into various horizons since the nitrogen and organic matter content varies with depth.

## Method of Procedure

### Shoot sampling

Total biomass and annual net biomass accumulation was determined for above-ground portions of higher plants in Eurotia and Atriplex communities. Total biomass estimates were made by removing, at ground level, the above-ground portions of all plants from plots sampled in a stratified random manner. Adhering soil particles and litter were removed from plants as they were clipped. Care was taken to insure adequate plot and sample sizes in all biomass sampling. A sample size of 15-20 plots from each plant community was found to be adequate to estimate mean above-ground biomass with an accuracy of about $\pm$ 15 percent with 90 percent probability.

Stands of Eurotia lanata are relatively small in stature and plants are evenly distributed, while stands of Atriplex confertifolia are larger in stature and the plants are much less evenly distributed. Because of these differences, a larger plot size was necessary for the Atriplex biomass sampling. Plot sizes of 1 $m^2$ for E. lanata and 4 $m^2$ for A. confertifolia were found to be adequate.

### Estimation of net above-ground productivity

Net annaul above-ground biomass and nitrogen was estimated by a technique which utilized the ratio of old and new growth of randomly selected individual plants from the plant populations of each plant community. Immediately before the above-ground plant biomass was to be removed, about 40 individual shoots were randomly selected from each stand. These plants were clipped at ground level. Care was taken

to remove any soil and adhering litter from the lower parts of stems. The plants were then carefully separated into old growth (OG) and new growth (NG) fractions.

New growth consisted of new twig and leaf production of the current growing season. Old growth consisted of stem biomass resulting from growth of previous years as well as the annual wood increment of the current year. Fall regrowth, induced by late summer rains, did not occur after sampling in 1968, 1969, or 1970. The Atriplex and Eurotia genera possess an anomalous pattern of stem growth characteristic of the Chenopodiaceae family. Therefore, it was impossible to separate or even estimate the current annual increment of new growth in stems more than one year old as has been done in previous studies in forest ecosystems (Whittaker and Woodwell, 1968).

Ratios of OG/NG were determined on a dry weight basis for each sample stem in a manner similar to that employed by Whittaker (1961) for estimation of net primary production in understory shrubs. Enough plants were sampled to estimate the mean ratio between old and new growth within about $\pm$ 10 percent of the mean at the 90 percent probability level. Annual net above-ground biomass accumulation was calculated by the application of the respective OG/NG ratios to the above-ground plant biomass estimates for each community.

Litter sampling

After the above-ground portions of all plants had been removed from a plot, litter was collected from the soil surface. The litter of the A. confertifolia community was collected into two conveniently separated fractions. One contained fine, easily decomposable leaves, very fine stems and animal feces (Atco fine litter); while the other

contained more resistant, coarse woody material (Atco coarse litter). E. lanata litter was all of a much finer consistency and thus was not separated into fractions. The litter collection process required that the surface soil of each plot be pulverized to reduce the size of soil aggregates to facilitate the separation of soil and small litter particles. This soil-litter mixture was partially separated with the aid of a seive. Openings in the seive were 1.6 mm in size. A known fraction of the soil-litter mixture was subsequently washed to remove soil particles completely. Dry weights were determined for fractional subsamples of litter after which the dry weight value of the entire litter sample from a particular plot was adjusted according to the subsample ratio. Plot sizes used for above-ground plant biomass sampling proved to be adequate for litter biomass sampling.

Root biomass sampling

Root biomass was determined from random core samples drilled in each sampling plot. Root sampling cores, 8.35 cm in diameter and 90 cm deep, were obtained by the use of a sharpened orchard auger. Root and soil mistures from 2-30, 30-60 and 60-90 cm depths were either placed in separate plastic bags to prevent drying before separation or were separated immediately in the field. Complete separation of the roots from soil was achieved by repeated gentle immersion of the root sample in clean water after it had been skimmed from the surface of a pan containing water and the agitated soil-root mixture. A small soil seive served as a temporary receptacle for roots between the skimming and final soil-root separation. The separation technique is similar

to one used by McKell, Wilson, and Jones (1961) in that flotation is used to separate roots from soil. However, good recovery of fragile and very fine roots of desert plants could be attained only by careful hand washing. Special care was exercised to prevent loss of small roots while washing away adhering soil particles. To dislodge soil particles the root samples were repeatedly pressed by hand against the screen of the temporary holding seive. This seive was then suspended in a larger pan of clean water and gently agitated to allow remaining loosened soil particles to fall through openings in the seive. By the use of this technique, soil was easily removed and very small roots which fell through the seive could be recovered by skimming them from the surface of the pan containing clean water. The separation of roots and soil was facilitated by the silt loam to sandy loam soil texture of the study plots.

Soil sample procurement

Soil samples were collected for nitrogen analysis. These samples were collected from the 0-2, 2-30, 30-60, and 60-90 cm depths. Soil from the 0-2 cm depth was obtained from soil screened from the soil-litter mixture and represents approximately the upper 2 cm of the soil profile. An orchard auger was used to collect soil core samples from the lower three sampling depths. Core samples for nitrogen analysis were drilled in a random pattern within each biomass sampling plot. All soil samples were seived through a 1.6 mm seive and only enough soil for gravimetric soil moisture and nitrogen determinations was collected. The remainder of the soil-root mixture was discarded into the drill hole.

Soil bulk density determination

Soil bulk density determinations for each plant community was necessary to express soil nitrogen values on a volume basis. Soil samples were collected in much the same manner as for routine sampling for soil nitrogen. Collection procedures differed only for the 0-2 cm depth. Soil bulk density for the 0-2 cm depth was collected in a core sampler which was pressed into the soil surface to a depth of 2 cm. A spatula was then inserted into the soil across the opening of the core sampler to prevent the sample from falling out as it was removed from the soil profile. Soil from the 2-30, 30-60, and 60-90 cm depths was carefully removed with the aid of an orchard auger which drilled a core of known diameter and depth.

Oven-dry weights for each segment were determined. The relationship between soil weight and core volume was calculated and the result expressed in $g/cm^3$ of soil.

Sample preparation

Plant, litter, and soil samples were prepared for total nitrogen analysis. Plant and litter samples were dried at 60 C for at least 48 hours, weighed, and ground to 40 mesh in a Wiley Mill. Care was taken to prevent reabsorption of moisture from the air by these highly hygroscopic materials by storage in air tight containers or by redrying prior to weighing for analysis.

Soil samples were dried at room temperature since it was found that all but about 1.5% moisture could be uniformly removed by this procedure. Drying at low temperature also prevented loss of inorganic soil nitrogen due to volatilization at high temperature and high pH.

To facilitate rapid drying, soil in paper bags was placed on a laboratory bench with ample space between each bag to allow for adequate air circulation.

Total nitrogen analysis

Semimicro-Kjeldahl methods were used to determine the nitrogen content of all plant and soil samples. Analysis procedures used were those suggested by Bremner (1965). The following procedure was used in all total nitrogen determinations. Amounts of soil and plant material used in the analysis were 2.0 and 0.2 g respectively. The sample for analysis was placed in a 100 ml digestion flask to which was added 2.0 g of digestion mix, containing $K_2SO_4$, $CuSO_4$, and selenium metal powder in a ratio of 100:10:1, and 6.0 ml of concentrated sulfuric acid. Digestion was initiated at low heat for the period of time required for rapid evolution of acid fumes to be completed. The temperature was then raised until the acid of the digest condensed about one-third of the way up the neck of the Kjeldahl flask. Digestion was continued for about one hour after the contents of the flask had cleared. After completion of the digestion process, the flask was allowed to cool. At this point 30 ml of distilled water was added to prevent solidification of digested sample in the bottom of the flask and to facilitate its transfer to the steam distillation apparatus.

Steam distillation

A self flushing steam distillation apparatus was used to recover the ammonia contained in salts produced by the acid digestion of the sample. The contents of the digestion flask were transferred to the chamber of the distillation apparatus after which the digestion flask

was rinsed three times with 10 ml of distilled water to complete the transfer. Ten ml of 2 percent boric acid solution, containing a bromocresol green and methyl red mixed indicator, was added to a 125 ml Erlenmeyer flask and placed under the condensor of the distillation apparatus so that the end of the condensor was about 4 cm above the surface of the boric acid solution. At this point, 25 ml of 10 N NaOH was added to the distillation chamber and distillation commenced. Distillation was completed when the distillate reached the 50 ml mark in the receiving flask. Nitrogen collected in the boric acid solution was titrated directly with the aid of the mixed pH indicators contained therein and 0.05 N sulfuric acid.

Residual solution in the distillation chamber was automatically removed from the unit under suction produced by steam condensing in the steam trap, whereupon the residue was allowed to drain from the unit by opening a valve at the bottom of the trap. At this point the steam distillation unit was ready to receive and distill another digested nitrogen-containing sample.

Determination of organic carbon and total soluble salts in soils

Organic carbon in soils was determined using the modified Schollenberger method (Schollenberger, 1927; Jackson, 1958). Carbon was determined by wet combustion in an excess of potassium dichromate solution. Excess dichromate was reduced by addition of ferrous ammonium sulfate solution which in turn was titrated with standardized potassium permanganate solution. The difference between the amount of standardized potassium permanganate used in titrating blanks and soil samples served as the basis for calculation of organic carbon. Since soil

samples contained appreciable quantities of carbonate and chloride salts, concentrated sulfuric acid, containing 25 g of silver sulfate per 1, was used to drive off inorganic carbonates and prevent interference of chlorides by precipitation with silver ion.

Total soluble salt content of soil samples from various depths in each plant community was determined with a Beckman Model RC 16B2 conductivity bridge in conjunction with a Model CEL-M soil cup. The resistance of a soil paste was adjusted for temperature and then converted to percent salt according to method 5 (U. S. Salinity Laboratory, 1954).

## Results

Results of total biomass and nitrogen inventories for the years 1968-70 are presented in Table 1. Mean estimates of nitrogen in above and below-ground plant biomass, annual productivity, litter and soil to 90 cm depth are presented. Similar estimates of above-ground biomass and annual above-ground productivity, calculated from OG/NG ratios (Table 2) for individual years are presented in appendix Table 7. Estimates of root biomass in Eurotia and Atriplex plant communities for individual years are presented in appendix Table 8. Differences in Eurotia and Atriplex root biomass distribution with depth and the relationship between root growth and biomass accumulation and soil salinity are illustrated in Figure 3.

Total soil nitrogen and percent organic carbon were found to decrease in parallel fashion with depth (Figure 4) and calculated organic carbon:nitrogen ratios are presented in Table 3.

Table 1. Mean estimates for biomass and nitrogen in kg/ha in Atriplex confertifolia and Eurotia lanata salt desert shrub plant communities for the years 1968-70.

| Item | Depth (cm) | Eurotia lanata Biomass kg/ha | Eurotia lanata mg N/gm dry wt. | Eurotia lanata kg N /ha | Atriplex confertifolia Biomass kg/ha | Atriplex confertifolia mg N/gm dry wt. | Atriplex confertifolia kg N /ha |
|---|---|---|---|---|---|---|---|
| Above-ground biomass | -- | -2410- | 11.90 | -28.7- | -4170- | 11.30 | -47.1- |
| New growth | -- | 700 | 12.85 | 9.0 | 840 | 14.62 | 12.3 |
| Old growth | -- | 1710 | 11.08 | 18.9 | 3330 | 9.94 | 33.1 |
| Fine litter | -- | -4000- | 14.14 | -56.6- | -4030* | 13.27 | -53.5- |
| Coarse litter | -- | ---- | ----- | ---- | -4460- | 9.93 | -44.3- |
| Below-ground biomass | 2-30 | 7210 | 15.96 | 115 | 9450 | 16.62 | 157 |
| | 30-60 | 6680 | 15.68 | 105 | 2920 | 17.71 | 52 |
| | 60-90 | 2180 | 17.95 | 39 | 760 | 19.81 | 15 |
| | | -16,070- | | -259- | -13,130- | | -224- |
| Biomass & Litter | | -22,480- | | -344- | -25,790- | | -369- |
| Soil nitrogen | | Bulk Density | mg N/gm dry wt. | kg N /ha | Bulk Density | mg N/gm dry wt. | kg N /ha |
| | 0-2 | 1.14 | 1.50 | 344 | 1.18 | 1.78 | 425 |
| | 2-30 | 1.10 | 0.80 | 2460 | 1.20 | 0.83 | 2780 |
| | 30-60 | 1.24 | 0.66 | 2460 | 1.23 | 0.74 | 2720 |
| | 60-90 | 1.42 | 0.53 | 2260 | 1.25 | 0.66 | 2480 |
| | | | | -7524- | | | -8305- |
| Community Nitrogen Totals (Biomass + Litter + Soil) | | | | -7868- | | | -8674- |

*Mean of 1968-69 data only

Table 2. Average old growth:new growth ratios for Eurotia lanata and Atriplex confertifolia above-ground biomass during the years 1968-70.

| Year | Plant Community | |
|---|---|---|
| | Eurotia lanata | Atriplex confertifolia |
| 1968 | 1.676 | 3.850 |
| 1969 | 3.528 | 6.847 |
| 1970 | 2.587 | 2.497 |

Table 3. Organic carbon:nitrogen ratios of Eurotia and Atriplex soils.

| Depth (cm | Soil Carbon : Nitrogen Ratios | |
|---|---|---|
| | E. lanata | A. confertifolia |
| 0-2 | 10.7 | 10.5 |
| 2-30 | 11.9 | 10.8 |
| 30-60 | 12.3 | 13.2 |
| 60-90 | 15.7 | 13.3 |

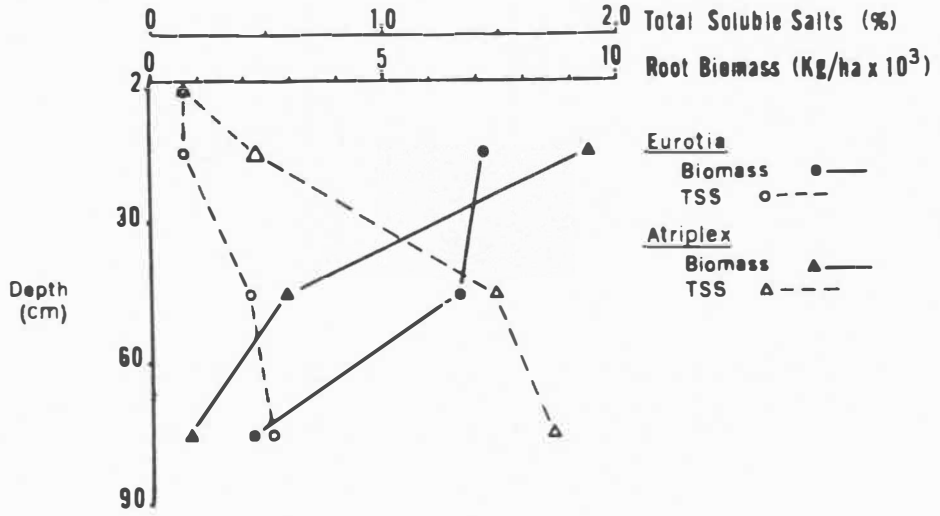



Figure 3. The vertical distribution of root biomass and total soluble salts (TTS) in the soil profiles of Eurotia and Atriplex plant communities.

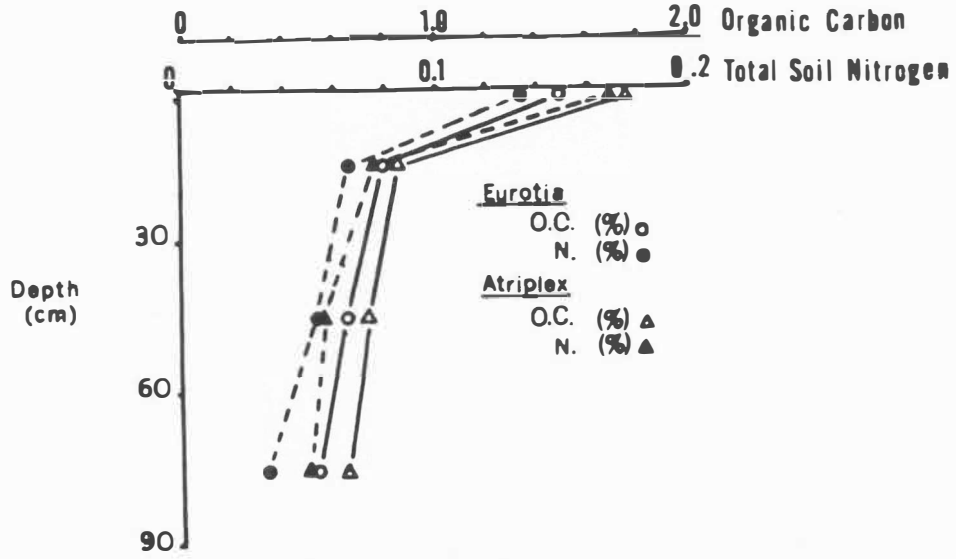



Figure 4. The vertical distribution of organic carbon and total soil nitrogen in the soil profiles of Eurotia and Atriplex plant communities.

Separate statistical analyses of biomass data are presented in appendix Tables 9 through 13. Briefly, significant differences exist between plant communities for above and below-ground biomass and associated nitrogen, litter and associated nitrogen, and the distribution of total nitrogen in the soil profiles of the respective plant communities. Table 8a provides means, sample sizes, and standard deviations for biomass sampling in Eurotia and Atriplex plant communities during the years 1968-70.

## Discussion

### Basic assumptions and long-term considerations

Due to nearly constant moisture stress, plant communities of arid regions are limited with respect to the amount and duration of transpiring above-ground tissues which can be displayed. Root systems tend to be larger in areal extent and possess greater biomass than above-ground portions of plants, often accounting for up to 80-90 percent of the total plant biomass (phytomass) (Bazilevich and Rodin, 1968). Because of this biomass relationship between above and below-ground portions of desert plants, there is a limitation in the areal extent of canopy cover and plant density imposed by vigorous competition among large and extensive root systems for soil moisture. Thus in desert ecosystems, soil moisture stress and a limited amount of photosynthetic tissue combine to limit net productivity. Walter (1954) has shown that dry matter production in deserts is a linear function of rainfall up to 600 mm and that average annual primary productivity of true deserts is less than 2000 kg/ha. Hutchings and Stewart (1953) have also shown that herbage production can be reliably predicted by precipitation

during the preceding twelve months at the Desert Experimental Range in western Utah.

Ecologists generally agree that plant succession in desert ecosystems is a relatively slow process compared to more mesic environments. However, owing to the relatively long developmental period these salt desert shrub communities have undergone since late Pleistocene (Bright, 1966; Harper and Alder, 1971), it is assumed that near steady state conditions should exist between vegetation and climate.

With the above-ground biomass limitation and the existence of an equilibrium between vegetation and climate, several other conditions are likely to exist with respect to the size and transformation rates among nitrogen-containing compartments in the ecosystem. Most important is that, in a long term situation, there will be little change in the absolute size of nitrogen-containing compartments, including above and below-ground plant biomass, litter, and soil. Under these conditions, average net annual productivity and associated nitrogen uptake is equivalent to average annual organic matter and nitrogen increment in litter fall of shoots and roots. Average litter fall in turn is equal to average annual litter decomposition and transformation of nitrogen to inorganic forms which are again made available for plant uptake.

These relationships may be subject to modification by the following: (1) removal of plant biomass by herbivores and conversion of the associated nitrogen to new organic compounds, some of which may not be returned to the ecosystem through excreta of upon death and decomposition of the animal, (2) loss of nitrogen through leaching, volatilization and denitrification of inorganic nitrogen compounds and, (3) loss of organically incorporated nitrogen to accelerated erosion.

An attempt was made to minimize and evaluate the effects of these factors upon the system studied by the following: (1) the study areas, which had been ungrazed by domestic livestock for two years, were fenced to prevent further domestic livestock use and to minimize other disturbance factors, principally excessive grazing by rabbits, (2) the study sites were chosen on the basis of their good condition and lack of apparent recent disturbance, and (3) a nitrogen fixation investigation was undertaken to determine whether inputs of new nitrogen were being received by the ecosystem which would offset losses of inorganic nitrogen from the system.

Plant nitrogen and biomass comparisons

The plant communities studied were chosen on the basis of contrasting autecology of the dominant plants which is evident in growth habit, size and spacing of plants, and timing of phenological events. However, if total amount of plant biomass in each community (see Table 1) are compared, very small community differences are evident. Only about 1000 kg/ha more biomass and less than 20 kg/ha more nitrogen occur in the Eurotia community compared to the Atriplex community. These differences are small and well within the range of sampling error. This finding strengthens the assumption of an overall vegetation-climate equilibrium in the study area.

When the plant biomass in each community is subdivided into its respective parts, large differences are apparent. These might be expected due to the contrasting autecology of the dominant plant species. For example, mean estimates of nitrogen and biomass in the above-ground portions of the Atriplex community are nearly twice those in the Eurotia community.

The range of above and below-ground biomass estimates for these cold desert plant communities seem to agree quite well with those of similar arid regions in other parts of the world (Whittaker, 1970: Basilevich and Rodin, 1968).

Litter and associated nitrogen

Estimates of litter and associated nitrogen show the same relationship as is found in the above-ground plant parts. The Atriplex community contains nearly twice the amount of litter and associated nitrogen as can be found in the Eurotia community (see Tables 1 and 7).

The litter of the Eurotia community consists, for the most part, of fine stems and leaves of high nitrogen content in various stages of decomposition. The litter of the Atriplex community, however, can be separated into two distinct components from the standpoint of nitrogen content and susceptibility to rapid decomposition. One component consists of easily decomposable fine stems and leaves, comparable to Eurotia litter, while the other consists of highly resistant coarse woody material.

Again, reasons for the large differences in litter mass are easily accounted for by the differences in size and growth habits of the respective dominants. This is evidenced quantitatively by significant differences in overall OG/NG ratios between communities (Table 2); i.e., relative amounts of old stem versus new twig and leaf growth. Atriplex plants are larger in stature, have stems of greater diameter and length, and possess definite shrubby appearance compared to Eurotia plants. Eurotia plants, by comparison, are low,

fine stemmed, half-shrubs. Both species retain at least part of their leaves throughout the entire year, but no leaves remain alive more than one year on either plant species. Because of growth habit, sections of Atriplex plants, lost as a part of periodic die back, have a larger proportion of coarse woody material than Eurotia plants as evidenced by litter composition.

In either community the nitrogen concentration of litter of fine composition (Eula litter and Atco fine litter) is greater than in above-ground biomass. In the Eurotia community, litter nitrogen concentration even exceeds the nitrogen concentration of new leaf and twig growth (Table 1). Thus a biological concentration of nitrogen in litter and its residues during decomposition is readily apparent as carbon is dispersed as $CO_2$ during decomposition and nitrogen is retained in organic forms. The coarse litter of the Atriplex community, which occurs in equally large quantities (Table 1) has a much lower nitrogen concentration and appears to decompose very slowly as evidenced by lichen establishment upon its exposed surfaces. Obviously, the litter fall, decomposition, and nitrogen turnover rates in the coarse litter component are much slower than for litter of finer composition and higher nitrogen concentration.

## Above-ground annual productivity

Estimates of mean annual productivity for above-ground portions of plants and associated nitrogen are, by comparison (Tables 1 and 7), more nearly equal in the two communities than are estimates of total above-ground biomass. Estimates of annual above-ground productivity and associated nitrogen, based upon OG/NG ratios (Table

2), are about 3 and 140 kg/ha greater respectively in the Atriplex as compared to the Eurotia community. Further comparison shows that the Atriplex community has a 3-year average of 73 percent more above-ground biomass but only 20 percent greater annual twig and leaf growth. This actively transpiring new leaf and twig growth roughly corresponds to the herbage production measured by Hutchings and Stewart (1953). Thus the development of new above-ground tissues is closely related to available soil moisture. Since Eurotia and Atriplex communities receive about the same annual precipitation, comparable amounts of new growth might be expected to develop in each community.

Accumulation of transported photosynthate in the new wood increments on old stems and in roots, on the other hand, may be influenced more strongly by plant growth habit. Biomass estimates indicate that a large amount of the photosynthate produced by photosynthetic leaf and twig tissue has been transported to old stems and roots where its accumulation can not be measured by experimental methods used in this investigation. More detailed evaluation would require radioactive tracers such as those used to Dahlman and Kucera (1968) in a prairie ecosystem. Methods such as this can also be used to study the subsequent transfer of the tracer among different compartments of the ecosystem (Dahlman and Kucera, 1967). Since it is apparent that Atriplex and Eurotia plants are apportioning unmeasured photosynthate and nitrogen in varying amounts to different plant parts, such improved methodology could readily account for differences in root and shoot biomass between plant communities. However, based upon the data at hand, it appears that

net annual productivity and associated nitrogen transformations in each community are roughly equivalent when new leaf and twig growth and total plant biomass are used as indicators.

The present study shows that very small amounts of nitrogen are incorporated into annual above-ground production in both plant communities (Tables 1 and 7). Compared to the amount present in the entire ecosystem, only about 0.3-0.6 percent of the biologically incorporated nitrogen can be found in above-ground portions of plants; and of this amount only about one-third is found to be associated with new leaf and twig growth. Assuming that steady state conditions exist; i.e., that average annual above-ground production is equal to average annual litter fall, there is an approximate litter nitrogen turnover rate of 6.3 and 4.4 years for Eurotia and Atriplex communities respectively if Eurotia litter and Atriplex fine litter are considered. When both Atriplex coarse and fine litter are taken into account, the turnover rate is about 8.0 years for Atriplex community. Since decomposition of Atriplex coarse litter is very slow, the mean rate value for total litter nitrogen turnover probably lies somewhere between 4.4 and 8.0 years.

Root biomass and associated nitrogen

Mean estimates of root biomass in Eurotia and Atriplex communities were significantly different (Tables 1 and 8; Figure 3). Root biomass in the Eurotia community is about 3000 kg/ha greater than the Atriplex community when total mean values are compared. This difference more than compensates for the greater above-ground biomass in the Atriplex community and results in roughly equivalent total plant biomass in the two communities.

Large differences exist between communities in the distribution of root biomass and associated nitrogen within the soil profile (Tables 1 and 8). The Eurotia community appears to be more uniformly rooted with depth, especially within the 2-30 and 30-60 cm depths. Overall averages show a relatively small decrease in root biomass with depth in the Eurotia community compared to the Atriplex community (see Figure 3). Between 2-30 cm depth, root biomass in the Atriplex community is 1200 kg/ha greater than in the Eurotia community, whereas Atriplex root biomass is roughly only one-half that of the Eurotia community within the 30-60 and 60-90 cm depths. In both plant communities there is a precipitous decrease of root biomass within the 60-90 cm depth. Although some roots extend below 90 cm in both plant communities, their biomass is very small (Gasto, 1969) and their distribution is sporadic. Soil salinity, which produces a high osmotic potential at this level in the soil profile (R. T. Moore, 1971, personal communication), probably limits plant soil moisture uptake and ultimately root growth.

Root biomass distribution in the soil profile is probably controlled by several factors. First, there may be innate differences in rooting habit of the dominant species rooted in exactly equivalent soil profiles. Secondly, soil texture may affect root distribution through its influence on soil moisture retention and vertical distribution. The soil of the Atriplex community has a finer texture and has better developed structural characteristics and therefore greater moisture retention capacity than the Eurotia soil (Figures 10 and 11). For this reason, moisture does not penetrate as deeply in the Atriplex soil (Gasto, 1969). It follows that root growth and biomass should be greatest in the upper part of the Atriplex soil profile where moisture

tends to be most readily available. A third factor which may differentially affect root distribution is the concentration of soluble salts in the soil profile. Findings by Gates (1956) and by Gates, Stoddart, and Cook (1956) indicate that Atriplex confertifolia soils usually have a greater concentration of soluble salts and exchangeable sodium and a greater field capacity for soil moisture than Eurotia lanata soils. Results of total soluble salt determination (Figure 3) indicate that large differences in soluble salt concentration with depth exist between plant communities. There appears to be a minimal amount of soluble salts in the surface 2 cm of soil of both communities because of leaching. Greater field capacity in the finer-textured Atriplex soil limits moisture penetration and the leaching of soluble salts. Thus high salt concentrations and unfavorable osmotic conditions are encountered at shallower depths. The coarser-textured and less retentive Eurotia soil, on the other hand, shows the effects of greater leaching in the upper parts of the soil profile and an abrupt increase in salinity at about the 50 cm level, marked by a definite carbonate accumulation. Figure 3 also shows that roots are allowed to proliferate in the greatest quantities where osmotic potential is least limiting, namely near the surface, and that salinity is least limiting in the Eurotia soil. Thus it is concluded that soil texture and its ultimate effects upon soil moisture retention and redistribution of soluble salts in the soil profile appears to be the factor most responsible for differences in root distribution between plant communities.

The nitrogen concentration of root biomass varies between communities and with sampling depth. In general, the nitrogen concentration of Atriplex roots is slightly greater than Eurotia roots (Tables 1 and 8).

In the Atriplex community root nitrogen concentration increases consistently with increasing depth; however, in the Eurotia community the lowest and highest root nitrogen concentrations are found at the 30-60 and 60-90 cm depths respectively; the 2-30 cm depth is intermediate in all cases.

During root sampling, time did not permit a separation of root biomass from dead root litter. Root litter was, however, observed in all root samples, but seldom did its presence indicate it to be the most conspicuous component of a particular sample. Root litter appeared to predominate only when a randomly located coring sampled the root crown of a dead plant. Among live roots, dead corky tissue accounts for the greatest part of root volume since they possess only a tiny core of light-colored conductive tissue. The latter characteristic serves to distinguish between live and dead roots and gives live roots a greater degree of structural integrity.

Roots were not found in the surface 3-5 cm of soil in either plant community. This portion of the soil is subject to rapidly fluctuating soil moisture and temperature conditions. Both factors undoubtedly interact to make the maintenance of perennial root biomass at this level in the soil profile impossible.

Comparison of above and below-ground biomass estimates revealed that a great preponderance of below-ground biomass exists. Mean values for three annual biomass and nitrogen inventories indicate that below-ground biomass accounts for 87 and 74 percent of the total biomass in Eurotia and Atriplex communities respectively. If the above-ground biomass and litter are compared to root biomass; roots account for 71 and 51 percent of the combined living and dead organic material in Eurotia and Atriplex plant communities.

Soil nitrogen

The soils of salt desert shrub communities are relatively poor in nitrogen compared to soil of more mesic environments and approach the nitrogen concentration of many agricultural and moist grassland soils only in the upper 2 cm of the soil profile. Nitrogen concentration of salt desert shrub surface soils is equivalent to the average nitrogen concentration of agricultural soils (Marbut, 1935). However, when equal volumes of soil are considered, desert soils may contain far less nitrogen because of a sharp decrease in nitrogen concentration with depth.

In general the nitrogen concentration of Eurotia and Atriplex soils is relatively high within the 0-2 cm layer above the rooting zone and decreases rather rapidly to about one-half of the surface value in the 2-30 cm zone. The decrease in nitrogen and organic carbon is nearly linear according to the mean values for the lower three sampling depths (see Figure 4). The greatest difference in total soil nitrogen between communities appears to be in the 0-2 cm of surface soil. In this part of the soil profile the Atriplex community contains about 24 percent more nitrogen on a volume basis. For the remaining three sampling depths total nitrogen in the Atriplex community is greater by 13, 10.5, and 10.3 percent respectively. These differences, in large part, may be due to soil texture. A sandy soil usually carries less organic matter and nitrogen than one of finer texture (Buckman and Brady, 1960). This is probably due to the lower moisture content and to the greater tendency for oxidation in these lighter soils.

Carbon:nitrogen ratios in the soils of the two plant communities are quite similar with the greatest differences between communities

occurring at lower depths (Table 3). All C:N ratio estimates, except one for the 60-90 cm zone in the Eurotia community, fall within the range of 8:1 to 15:1 commonly found in arable soils. Mean C:N ratio estimates for 0-2 and 2-30 cm depths of both communities are within the median range of between 10 and 12:1 reported by Buckman and Brady (1960). The C:N ratios of salt desert shrub soils differ from soils of other areas in that the ratios for subsurface parts of the profile are greater, rather than smaller, than for the corresponding surface layers. The added environmental stress of high soil salinity may be the factor responsible for this difference, which in areas of equal rainfall is often caused by cooler temperatures.

The soils of both communities are, by far, the largest reservoirs of nitrogen and organic matter in the ecosystem. Given, that the ratio between organic carbon and organic matter in the soil is very nearly constant at 1:1.7 (Buckman and Brady, 1960) and the mean C:N ratio of these salt desert shrub soils is 12.3, soil organic matter accounts for about 96 percent of the nitrogen and about 87 percent of the organic matter in a salt desert shrub ecosystem.

Even though the soils of salt desert shrub communities contain extremely large reservoirs of nitrogen and organic matter, the importance of this large nitrogen pool as a readily available source of inorganic nitrogen for higher plants must be qualified. Soil organic matter and associated nitrogen may be entirely microbial in origin (Kang and Felbeck, 1965) and thus a very stable terminal residue of decomposition not subject to further transformation of any consequence by microorganisms. If subject to appreciable decomposition, humus and associated nitrogen would not accumulate over long periods of time

in such great quantities as occur in soils of terrestrial ecosystems. Carbon dating of the organic matter in soil profiles lends even more credence to this hypothesis. According to Paul and co-workers (1964), soil dates to recent profiles that lie within the root zone are not identical with the absolute soil age. They characterize the equilibrium between old humus decomposition and young organic matter additions and have determined mean residence times of soil organic matter. According to carbon-14 dating techniques, mean residence times may be on the order of several thousand years.

On the other hand, decomposition tests on uniformly labeled new organic matter show residence times of only about one-tenth year (Scharpenseel, 1971). From these studies it appears that small quantities of nitrogen containing organic matter or its partially decomposed residues may serve as a more readily available source of nitrogen for plants than soil humus. In the light of this evidence, annual additions of plant litter fall to the soil of a terrestrial ecosystem are highly important for the maintenance of nitrogen fertility. The importance of litter and its decomposition products in surface soil is also indicated by the destructive and long-lasting effects caused by removal of surface soil by erosion (Cowling, 1969).

# CHAPTER III

# NITROGEN FIXATION BY SOIL SURFACE ORGANISMS

## Introduction

Close scrutiny of any terrestrial ecosystem will reveal that nitrogen-fixing organisms are always found to occupy certain biological niches and thus provide a renewable source of biologically available nitrogen for the system. The success of this evolutionary strategy for nitrogen fixation forms an important part of the nutritional basis for the productivity of the ecosystem. Generally, the nitrogen-fixing organisms in an ecosystem help to accumulate and maintain nitrogen fertility by replacing losses to leaching, erosion, denitrification, volatilization, and removal by domestic livestock grazing.

Cold deserts of the Intermountain region are often lacking in nitrogen-fixing leguminous species. Legumes present in some areas make up such a small part of the vegetation as to be of insignificant value as host plants for nitrogen fixing bacteria. In greenhouse experiments E. lanata and A. confertifolia plants were unable to grow in a nutrient media lacking available nitrogen and displayed characteristic nitrogen deficiency symptoms. They were, however, able to grow normally on nutrient media containing nitrate in addition to other essential elements.

According to Bond (1967) there are 13 genera of nonleguminous dicotyledonous woody plants, comprising about 310 species, which are host to nodulating root bacteria. However, no representatives of

these host genera are present in the study plots for this research or the surrounding areas.

Possible alternative sources of fixed nitrogen are the free-living heterotrophic bacteria of the genus Clostridium or the genus Azotobacter. The genus Clostridium is found in most fertile soils and requires strict anaerobic conditions for growth (Alexander, 1965). In microecological sites, such as the interior of water saturated soil crumbs, more than 3 mm in radius, facultative aerobes may reduce the partial pressure of oxygen to the level that strict anaerobes can proliferate (Alexander, 1965). However, since desert soils lack a high degree of fertility and are usually aerobic due to almost continually high moisture stress and lack the degree of soil crumb development necessary for anaerobic microsites, this avenue of nitrogen fixation is probably not a significant one in cold deserts.

Shields (1953) has suggested that Azotobacter is almost always absent in soils receiving less than 250 mm of precipitation annually and is infrequently present in areas of 375-500 mm rainfall. Techan and Beadle (1955) reported the input of nitrogen fixation by Azotobacter in semi-arid areas of Australia to be about 0.1 kg/ha/yr. Since the rainfall in the study area is usually less than 250 mm, nitrogen input from Azotobacter is probably insignificant.

Fletcher and Martin (1948), Cameron and Fuller (1960), Mayland, McIntosh and Fuller (1966), and Rogers, Lang and Nicholas (1966) have shown that lichens and blue-green algae of desert soil surface habitats may fix atmospheric nitrogen into biologically active forms. These organisms grow abundantly upon the soil surface in both study plots and in the surrounding area. This, coupled with information eliminating,

for all practical purposes, other sources of nitrogen in the ecosystem, suggested that lichens and blue-green algae might be responsible for nitrogen fixation in these salt desert shrub plant communities. Accordingly, an investigation was initiated in the spring of 1969 to evaluate the soil surface organisms (lichen and blue-green algae associations) of each plant community as a source of fixed nitrogen.

## Method of Procedure

### Collection of experimental material

Experimental material was collected from each plant community in the spring of 1969. Lichens and blue-green algae tend to stabilize the soil surface into a polygonal pattern of surface plates and these were conveniently removed from the soil surface in random fashion as a source of viable soil surface organisms for study (Figures 5 and 6).

Preliminary sampling indicated that surface polygons from Eurotia community to be very uniform in appearance and nitrogen content. Therefore, no attempt was made to separate this material in the experimental design. The experimental material from the Atriplex community appeared to be rather variable in appearance and nitrogen content. Therefore, a method was devised to reduce the variation among experimental units from this source. Surface polygons were separated into groups having relatively low and high lichen cover because earlier sampling had indicated nitrogen content to be positively correlated with lichen cover. The experimental units made from these surface crusts were designated either Atco-L (Atriplex, low lichen cover) or Atco-H (Atriplex, high lichen cover).

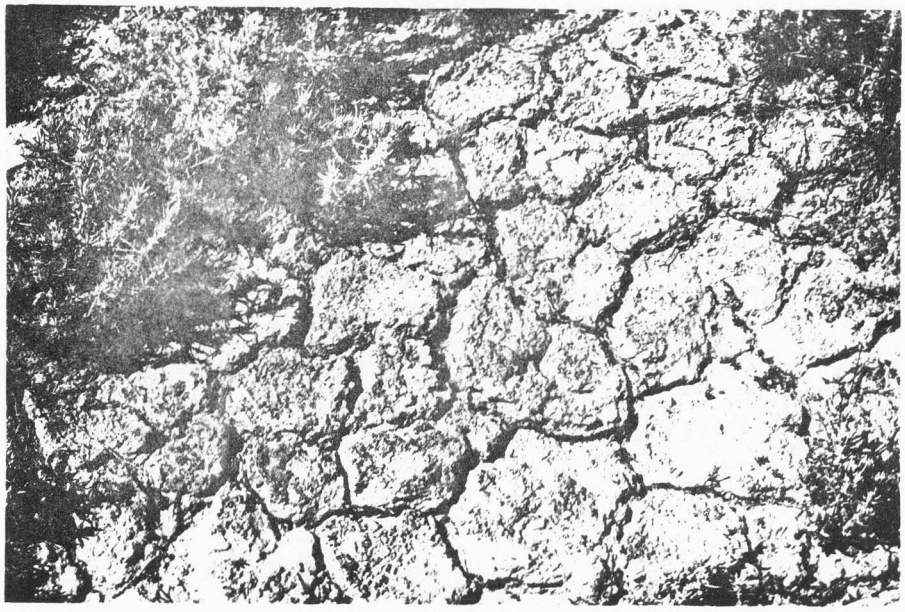


Figure 5. A close-up view of polygonal soil surface crusts in the Eurotia lanata community.

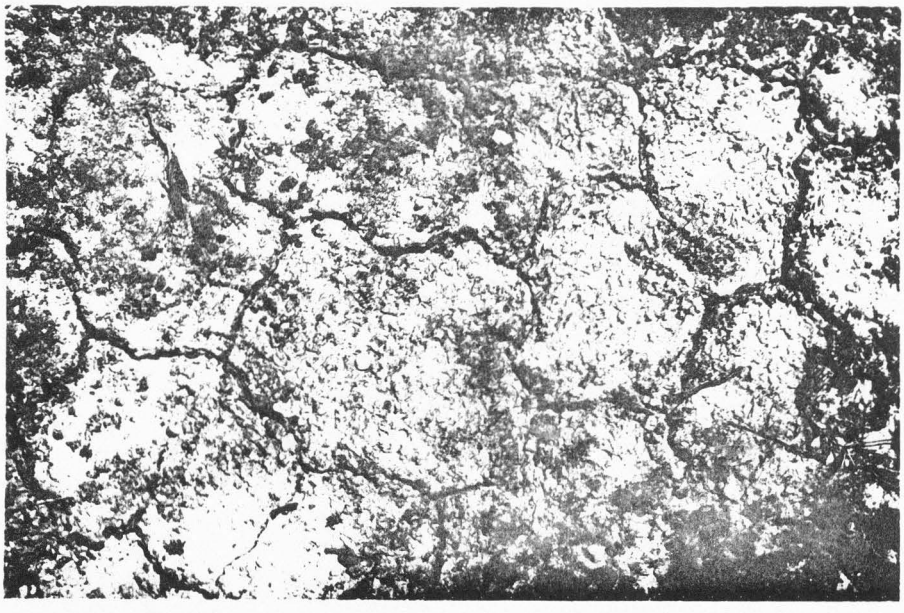


Figure 6. A close-up view of polygonal soil surface crusts in the Atriplex confertifolia community.

Composite soil surface samples were made of about 50 small pieces taken from many different surface plates from each of the three respective soil surface types; i.e., Eula, Atco-L, and Atco-H.

Methods for making composite samples were similar to those used by Mayland et al. (1966). Preliminary analysis indicated that six to eight of these experimental units were sufficient to estimate the mean nitrogen content of the soil surface within $\pm$ 10 percent with at least a 90 percent level of confidence. Composite experimental units were assembled in the following manner. The lower surface of each soil surface plate was abraded away on a screen until a thickness of approximately 0.5-1.0 cm was attained. Next the surface plates were moistened and cut into pieces about 2 $cm^2$ in area. The small pieces were subsequently fitted into a 8.9 x 11.8 cm clear plastic flat lined with polyethylene film. The composite experimental unit had an area of 104 $cm^2$ and a weight of approximately 70 g.

Incubation

Experimental units from the three sources (Eula, Atco-L and Atco-H) were equally divided among three treatments. These were control (dry) and two continuously wet incubation periods of 18 and 58 days respectively. With the exception of those experimental units from each source which served as the control treatment, all of the composited experimental units were placed in a large plexiglass incubation chamber for the growth phase of the experiment. The incubation chamber was located on a table in the center of a large growth chamber in which light and temperature environment could be controlled.

Daily growing conditions consisted of 16 hr days at 1000 f. c. with day and night temperatures of 21 and 10 C respectively. Gas exchange for the incubation chamber was provided by air from a compressed air line. This air was first scrubbed of possible oil and ammonia contamination by passage through concentrated $H_2SO_4$ (Fuller, Cameron and Racia, 1960) and then rehumidified by passage through hot distilled water before entering the chamber.

Composite samples were watered periodically with distilled water. A visual inspection of the cultures was made each day and when it became necessary to add water, only enough to saturate the soil substrate was applied.

Preparation for analysis

At the end of the incubation period for each treatment, the experimental units were air dried at room temperature, ground with mortar and pestle to pass a 20 mesh seive, and stored. Prior to nitrogen analysis, all of the experimental material was dried uniformly at 60 C to remove moisture accumulated due to the hygroscopic nature of the algal and lichen biomass contained therein.

## Results

Experimental results indicate a significant difference in nitrogen-fixing potential between soil surface microfloras of Atriplex and Eurotia plant communities. Only those experimental units composited from Atriplex soil surface were able to fix appreciable amounts of nitrogen (Tables 4 and 14). Under the same incubation conditions, those composited from Eurotia soil surface were found to lack nitrogen-fixing potential (Table 15). Findings of the experiment show a signifi-

Table 4. Experimental results of nitrogen fixation experiments utilizing surface crusts from Eurotia and Atriplex communities.

| Source | Incubation Time | Mean mg N per gm Soil | Stat. Test | % Change in N Content |
|---|---|---|---|---|
| Eula | 0 (1) | 1.201 | | |
| | 18 (2) | 1.200 | 1 vs 2 | -0.80 ns |
| | 58 (3) | 1.162 | 1 vs 3 | -3.25 ns |
| Atco-H | 0 (1) | 1.775 | | |
| | 18 (2) | 1.819 | 1 vs 2 | +2.48 ns |
| | | | 2 vs 3 | +8.24 * |
| | 58 (3) | 1.969 | 1 vs 3 | +10.93** |
| Atco-L | 0 (1) | 1.295 | | |
| | 18 (2) | 1.332 | 1 vs 2 | +2.86 ns |
| | | | 2 vs 3 | +23.50** |
| | 58 (3) | 1.621 | 1 vs 3 | +25.17** |

*Significant at .05 level
**Significant at .01 level

cant interaction to exist between Atriplex soil surface type (Atco-L and Atco-H) and incubation treatment (Table 14).

Experimental results generally agree with observations of culture growth patterns made during the course of incubation. Eurotia soil surface organisms grew rapidly during the early part of incubation, but after about two weeks the appearance of soil surface organisms deteriorated resulting in little surface biomass accumulation or nitrogen fixation. Atriplex soil surface organisms grew rapidly for the entire incubation period, were able to accumulate a considerable amount of algal biomass on the soil surface, and fixed significant amounts of atmospheric nitrogen.

## Discussion

### The natural soil surface environment

Eurotia and Atriplex plant communities possess very different substrate and microclimatic regimes for the growth of soil surface algal and lichen floras. Conditions at the soil surface in the Eurotia community are relatively uniform. The dominant Eurotia plants are small, usually about 2-3 dm in height, and evenly distributed. The result is a minimum of shading and microclimatic amelioration by vegetal cover. In addition, the soil surface has a fine sandy texture, which makes it a relatively unstable habitat for lichen establishment. These conditions combine to produce a uniform distribution of soil surface organisms on litter-free soil surface between plants (Figure 5). In these spaces, considerable algal growth may occur during periods of favorable conditions; however, lichen establishment and growth is conspiciously lacking. A small soil surface moss, tentatively identified

as a member of the genus Grimmia, occurs in both plant communities. Its growth is favored by microclimatic amelioration in the vicinity of shrubs.

Shrubs in the Atriplex community are larger and less evenly distributed. This results in a relatively variable, but generally more ameliorated microenvironment at the soil surface. An abundant cover of dark crustose lichens exists on a finer textured surface soil (Figure 6). Lichen and moss cover is most conspicuous within the microclimatic influence of shrubs. In highly exposed plant interspaces, lichen cover is less conspicuous. On these surfaces the greatest concentration of lichens may be found at the edges of surface soil polygons where surface cracks produce a more humid microenvironment.

In either plant community cryptogams, consisting of algae, lichens, and mosses, occupy nearly 100 percent of the soil surface exclusive of shrub and litter cover.

Growth dynamics

The soil surface organisms of both plant communities appear to be very responsive to environmental conditions favorable for growth. Thus, after only a few days of warm rainy weather, the soil surface in the study areas assumes a greenish hue due to rapid algal growth. Mosses are similarly stimulated.

Under laboratory conditions the soil surface often appeared green within 15 minutes after wetting. Once the soil surface was moistened, it readily became apparent that virtually all bare soil surface was occupied by some type of photoautotrophic organisms (Figures 7 and 8). Under incubation, algal growth was very rapid. After only

Figure 7. A close-up view of Eurotia lanata soil surface organisms near the end of the 58 day incubation period.

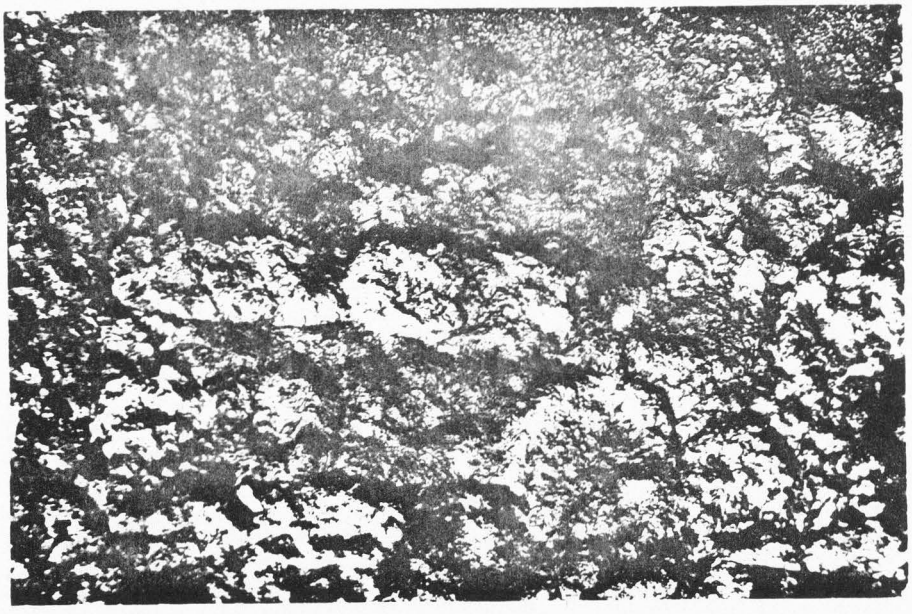


Figure 8. A close-up view of Atriplex confertifolia soil surface organisms near the end of the 58 day incubation period.

a few days, build-up of algal biomass imbeded in gelatinous sheaths became so extensive that it inhibited infiltration of water into the crust samples.

Soil surface organisms of Eurotia and Atriplex communities differed in their response to incubation conditions. Initially the algal species composition of both communities appeared to be nearly the same when algal species occupying virtually all of the Eurotia soil surface were compared to the algal flora of lichen interspaces of Atriplex soil surface. The main algal component was Microcoleus (Vouch) Gom. (R. I. Lynn, personal communication), a blue-green algae possessing thick gelatinous sheaths. Species of this genera are found world-wide, but lack nitrogen-fixing ability (Fuller, Cameron, and Racia, 1960). As the incubation progressed, the response of the soil surface organisms from the two communities differed conspicuously. Throughout almost the entire incubation period the main algal component of the Eurotia crusts, covering nearly 100 percent of their surface area, remained Microcoleus species. Late in incubation some small colonies of unidentified coccoid blue-green algae appeared; however, their origin may well have been contamination from sources exterior to the algal crust. Also, the existence of these colonies was never observed in the field and thus, even if they contained nitrogen-fixing algae, they could not be considered biologically important.

The vigorous response of the Atriplex soil surface microflora continued for the entire incubation period; however, algal species composition in lichen interspaces was found to vary considerably. After only a few days incubation, algal species containing heterocysts, commonly associated with nitrogen-fixing ability, were detected (Stewart,

Haystead, and Pearson, 1969). The most abundant of these was Scytonema (Kutz) which was first detected growing near abundant but very small and inconspicuous black crustose lichens typical of Atoc-L surface. Later, this algal species and another tentatively identified as Nostoc (Vouch) were commonly found growing in lichen interspaces. It has been suggested that lichens may serve as a reservoir for nitrogen-fixing algae which can grow into soil lichen interspaces during periods of favorable growth conditions (C. M. Wetmore, personal communication). Although heterocyst-containing algae were first found in near proximity to lichens, none were found to be lichen symbionts. It is not unlikely that a close association exists between lichen thalli and nitrogen-fixing algae even though an apparent symbiotic relationship does not exist.

Response to incubation treatment

Total nitrogen analysis of Eurotia soil crust samples incubated 18 and 58 days respectively indicated no net total nitrogen gain relative to dry control samples. For many experimental units there appeared to be an actual loss of nitrogen; however, comparison of treatment means indicated net losses to be insignificant (Table 4).

Soil surface organisms from the two Atriplex surface types were able to fix highly significant amounts of atmospheric nitrogen during 58 days of incubation. Estimates of atmospheric nitrogen fixation after only 18 days of incubation were greater than control, but differences were not statistically significant (Table 4). The Atco-L surface type showed the greatest increase in total nitrogen, about 25 percent during the 58-day incubation treatment, while the Atco-H surface type showed a smaller increase of approximately 10 percent.

The nitrogen concentration of salt desert shrub soil surface crusts initially brought in from the field appeared to be positively associated with the amount of lichen cover (Table 4). Indeed the near absence of soil lichens, lower soil crust nitrogen concentration in the field, and apparent lack of nitrogen fixation potential in the Eurotia soil surface compared to abundant soil lichens, greater crust nitrogen concentration, and significant nitrogen fixation in Atriplex soil surface indicate that nitrogen fixation potential may in some way be associated with the presence of lichens in soil surface crusts. In light of these observations, the greatest nitrogen fixation might be expected in surface crusts possessing the greatest lichen cover. However, the greater nitrogen-fixation response of the Atco-L surface type to the 58 day incubation period appears to contradict this hypothesis.

It is likely that the greater nitrogen fixation by Atco-L soil surface crusts may well be an artifact of the long laboratory incubation treatment. In the field, nitrogen-fixing algae, which appear to be closely associated with lichens, would have much less time to invade lichen interspaces normally occupied by algal species which do not fix nitrogen due to the very short periods of favorable growth conditions. It is likely that during long laboratory incubations, nitrogen-fixing species can more fully utilize lichen interspaces and thus fix greater amounts of nitrogen when lichen cover is less extensive. However, based on the nitrogen concentrations of field soil crust samples, the heavy lichen cover type appears to be most effective in accumulating nitrogen under natural conditions.

Ecological contribution of nitrogen fixation

Based upon the results of this experiment, one can postulate about

the amount of nitrogen fixation which might occur in the Atriplex community during the course of an annual cycle. The amount of nitrogen fixation per hectare can be calculated from the weight and area of the composite samples used in the investigation (Table 5). Values in this table are adjusted according to the amount of cryptogam covered soil surface area in the plant community.

Although a 10 to 25 percent increase was detected in experimental units incubated for 58 days, it is unreasonable to assume that the desert environment might have this many days of favorable soil surface conditions during the course of an annual cycle. As a result, nitrogen fixation values calculated on a per hectare basis for this incubation treatment are probably in excess of what might be measured in the field. The author has, however, observed very favorable soil surface conditions in summer lasting for periods of 2 to 3 weeks, which roughly corresponds to the 18-day incubation period. Although nitrogen increase in Atriplex experimental units was not statistically significant after the 18-day incubation period, it is most realistic to estimate the annual nitrogen fixation increment to be in the range indicated by this treatment. Depending upon growth conditions for soil surface organisms, the added increment for fixation would be in the 2-3 kg/ha range. Mayland et al. (1966) estimated nitrogen fixation of 10.7 kg per hectare of crusts per year in a desert grassland in southern Arizona. Since the algal crusts do not occupy the entire surface area under native conditions, nitrogen fixation would be less in situ. The desert grasslands of southern Arizona are a summer rainfall type and might be expected to provide a longer period of favorable soil surface

Table 5. Nitrogen fixation estimates by *Atriplex* soil surface crusts based upon 18 and 58 day incubation periods, a weight to surface area ratio of 0.675 $gm/cm^2$, and a soil surface cryptogam cover of 50 percent.

| *Atriplex* Soil Surface Type | Incubation (days) | Net $N_2$ Fixation (kg/ha of Crust) | Adjusted $N_2$ Fixation (kg/ha) |
|---|---|---|---|
| Atco-H | 18 | 3.0 | 1.5 |
| | 58 | 12.4 | 6.2 |
| Atco-L | 18 | 2.6 | 1.3 |
| | 58 | 21.9 | 11.0 |

growth conditions than the relatively dry summers of the northern Great Basin region.

An annual nitrogen input of 2-3 kg/ha is very small when compared to the total amount in the ecosystem. This raises the question of the ecological importance of such small inputs relative to the functioning of the entire system. Fogg (1947) and Mayland and McIntosh (1966) have shown that significant amounts of nitrogen fixed by blue-green algae is excreted. Laboratory experiments, utilizing higher plants in combination with nitrogen-fixing algae, have shown that excreted nitrogen is readily utilized by plants (Fuller, et al., 1960; Mayland and McIntosh, 1966). Assuming that excretion occurs during nitrogen fixation in desert soil surface crusts, nitrogen fixed would rapidly become available to higher plants. Because of low C:N ratios, (Fuller, et al. 1960), nitrogen incorporated into relatively short-lived algal biomass in soil-lichen interspaces should be rapidly released upon decomposition. The combined effects of excretion of fixed nitrogen and further nitrogen release upon decomposition, even though small, might produce an immediate beneficial effect upon salt desert shrub communities.

The surface soil on which nitrogen-fixing organisms are commonly found is also the zone of highest soil biological activity. Even though the total amount of nitrogen found there is small (Table 1), its high nitrogen concentration and rapid turnover rates could make it a readily available source of inorganic nitrogen for plant growth.

The nitrogen input from soil surface organisms may be important to ecosystem functioning in other ways. The ecosystem is subject to nitrogen loss in a number of ways. These may be loss to wind and water erosion, leaching beyond the reach of plant roots, volatilization of

ammonia, and loss to domestic grazing. Admittedly, these sources of nitrogen loss individually may be very small under natural conditions. However, taken collectively these sources of loss might easily equal the yearly input by nitrogen fixation. It is obvious that such a terrestrial ecosystem needs a source of nitrogen-fixation to maintain nitrogen fertility.

Therefore, even though the amount of nitrogen fixed annually by the surface microflora is small compared to the total organic nitrogen pool in the ecosystem, this fixation may be essential to the maintenance of the ecosystem in its present condition.

# CHAPTER IV

# INORGANIC SOIL NITROGEN

## Introduction

The dynamics of the nitrogen transformations in soil-water systems have been investigated in recent years (McLaren, 1969; Shaffer, Dutt, and Moore, 1970). Models describing inorganic soil nitrogen dynamics have been developed for these soil-water systems (McLaren, 1969; Shaffer, et al., 1970). However, there is little information relating to the inorganic soil nitrogen dynamics of intact, soil-water systems of natural terrestrial ecosystems. Such knowledge would naturally be of great utility for the integration of the various facets of the nitrogen cycle in desert plant communities. The vertical distribution pattern of inorganic soil nitrogen during the various seasons of the year coupled with a satisfactory measurement of downward nitrogen flux from litter and surface soil can be compared to indirect measures of nitrogen cycling rates and used to ascertain the degree of integration between ecosystem processes such as nitrogen mineralization and uptake of nitrogen by plants. Through collection and interpretation of this information a more complete understanding of the nitrogen cycle as it relates to ecosystem function can be obtained.

## Method of Procedure

### Soil sampling

Soil sampling methods used for collection of soil for inorganic soil nitrogen determinations were much the same as those described

earlier for the total nitrogen inventory. Sampling plots were chosen at random from transects and soil cores were collected at random within the confines of each plot. Soil was collected from 0-2, 2-30, 30-60, and 60-90 cm depths. At each collection date 10 complete cores were collected in each plant community and analyzed to estimate the inorganic soil nitrogen concentration at each sampling depth. Each plant community was sampled eleven times during a period of 25 months from April, 1968 to May, 1970. Sampling was most intensive during spring and early summer with a final annual sample collection just before the soil became frozen in November. Preliminary sampling indicated that inorganic soil nitrogen concentration might be related to soil moisture levels. Accordingly, simultaneous soil moisture and inorganic nitrogen sampling was initiated during the spring of 1969 and continued for the remainder of the sampling period.

Sample preparation

At the time of collection a small amount of well mixed soil from each sampling depth was seived through a 1.6 mm screen to remove plant roots. As a further precaution against contamination by nonsoil components, only enough soil for gravimetric soil moisture determination and inorganic nitrogen analysis was collected. This amounted to about 300 g of soil per sampling depth and the remainder of the soil-root mixture was discarded into the drill hole.

Soil samples for inroganic soil nitrogen analysis were dried at room temperature in paper bags. To speed the drying process, the bags were well spaced on a laboratory bench to allow for free air circulation.

Inorganic soil nitrogen flux

A satisfactory method of measuring the inorganic soil nitrogen flux from soil and litter above the rooting zone is difficult to implement. A method utilizing a "standardized soil cylinder" has been applied with some success (Klemmedson, et al., 1966). Metal cylinders filled with soil of known inorganic nitrogen concentration were used to collect inorganic soil nitrogen leached from decomposing litter and surface soil. The added inorganic soil nitrogen increment collected in the cylinder was determined by subtracting the initial from final inorganic soil nitrogen concentration. Since the inorganic nitrogen in surface soil leachate is not distributed evenly in each cylinder, soil must be removed in small increments and final and initial concentrations compared at each level. The result of this procedure gives an integrated incremental value for each experimental unit.

This type of experimental approach has some drawbacks which must be considered as one begins to interpret these experimental results. They are: (1) the difficulty of achieving good contact between the cylinder and surrounding soil, (2) the soil disturbance and alteration of initial conditions of moisture, temperature, and gas exchange, (3) the variability among experimental units due to uneven patterns of soil moisture infiltration, (4) the effects of abrupt changes in soil texture, bulk density, and matric potentials at the interface of the cylinder and surface soil, (5) the difficulty of excluding plant roots from feeding on inorganic soil nitrogen collected in the cylinder, (6) the exclusion of plant roots from the cylinder which results in higher soil moisture levels and therefore greater rates of nitrogen mineralization in the cylinder than is occurring in the surrounding soil.

Not withstanding the limitations of the method for measuring soil nitrogen flux, an investigation was carried out during the spring, summer, and fall of 1969 for the purpose of measuring soil inorganic nitrogen flux.

Standardized soil cylinders

Standardized soil cylinders were constructed and installed in the following manner. Soil was collected from the 0-20 cm depth in Eurotia and Atriplex communities. Plant roots and litter were removed with the aid of a 1.6 mm screen and the soil was temporarily stored in large plastic containers. The cylinder was constructed of aluminum beverage cans. After the ends of the cans were removed, they were thoroughly washed to prevent nitrogen contamination. A small inward fold was then made in the can end to be inserted into a lower segment in funnel fashion and the two were firmly rolled together with the aid of a heavy round steel bar. All joints were secured with plastic tape to strengthen the cylinder and prevent lateral moisture leakage during operation. The bottom of the cylinder was covered by glass wool which was held in place by nylon netting to hold soil in place and provide free gaseous exchange between the cylinder and soil profile.

Soil, previously collected for filling the cylinders, was thoroughly mixed and subsamples were taken to determine the initial inorganic nitrogen content. The soil was packed slightly more than in the undisturbed profile to prevent settling and loss of contact with the surface soil once the cylinders were installed. Due to packing, the bulk density of the soil cylinders was about 0.15 $g/cm^3$ (about 12 percent) greater than the soil in the undisturbed profile of the plant community.

The soil cylinders, standardized in the sense that the initial inorganic nitrogen content was known, were placed in the soil profiles of their respective plant communities July 1, 1969. Installation required the removal of a portion of the soil surface, either by removal of a lichen and algae stabilized soil surface polygon or removal of a section of soil-litter surface with a flat spade. A hole was drilled to accept the cylinder and the top of the cylinder was adjusted to a level about 5 cm below the soil surface. Soil from the hole was packed around the cylinder to insure good lateral contact after which the soil surface was replaced and the location was marked with a painted pot stake, offset about 15 cm. Equal numbers of cylinders were placed under bare and litter cover soil surface in each community.

One half of the cylinders were removed on November 15 of 1969 and the remainder in June of 1970. Immediately upon removal, soil was removed from each cylinder in increments which included 0-2.5, 2.5-5, 5-7.5, 7.5-10, 10-12.5, 12.5-17.5, 17.5-22.5, 22.5-27.5 and 27.5-32.5 cm. Since the cylinders were put together in three segments, soil removal was easily accomplished because successive can segments could be removed as soil was removed from the cylinder.

Inorganic soil nitrogen analysis

A potassium chloride extraction and steam distillation method was used to determine inorganic soil nitrogen concentrations in soil samples collected for this purpose. Analysis methods used were those recommended by Bremner and Keeney (1966).

The inorganic soil nitrogen analysis consisted of the following procedure. Forty grams of soil from a well-mixed sample was extracted

with 100 ml of 1.0 N KCl solution for one hour and then filtered. The filtrate was restored to 100 ml with KCl solution and 50 ml allequots were transferred to the chambers of two different distillation units. To one chamber was added 0.2 g of MgO to recover inorganic nitrogen in ammonia form and to the other chamber was added MgO and finely divided Devarda alloy. The latter reduces nitrate to ammonia so that all of the inorganic nitrogen in that fraction of the extract can be collected as ammonia. During distillation, ammonia was collected in 2 percent boric acid solution, containing a mixed indicator, after which the nitrogen in the distillate was titrated directly with 0.005 N sulfuric acid.

## Results

### Inorganic soil nitrogen dynamics

Experimental results for inorganic soil nitrogen dynamics are based upon the inorganic soil nitrogen (ISN) concentrations in ppm (wt) in Eurotia and Atriplex communities within four sampling depths at eleven dates during a period of 25 months. Inorganic soil nitrogen was fractionated during analysis and was recorded as three different quantities representing ammonia, nitrate, and total ISN (ammonia plus nitrate). Analysis of variance, utilizing a split plot design over time, was computed for values representing each ISN fraction (see Appendix Tables 16 and 17). Significant differences at the .01 level of probability were found at all levels within the experimental design for total ISN and nitrate; i.e., between communities, sampling dates, sampling depths and all interaction means (see Appendix Tables 16 and 17).

Ammonia, the remaining ISN fraction, showed no significant differences between plant community means and between means representing

the community x depth x sampling date interaction (see Appendix Table 18). Differences at all other levels of the experimental design were significant at the .01 level of probability. The results of inorganic soil nitrogen sampling are illustrated in graphic form in Figures 9, 10 and 11. Figure 9 illustrates total ISN concentration at each sampling depth over the entire sampling period. The more detailed Figures 10 and 11 illustrate concentrations of all three ISN fractions and concurrent soil moisture with depth over a shorter period of time from April, 1969, to May, 1970.

Inorganic soil nitrogen flux measurement

Inorganic soil nitrogen flux estimates are based upon net amounts of ISN collected in standardized soil cylinders, positioned to collect soluble nitrogenous compounds, principally nitrate, entering the rooting zone. Analysis of variance (Table 19) shows significant differences in ISN flux between plant communities and between standardized cylinders under litter-covered and bare soil surfaces within plant communities.

Total ISN entering the rooting zone from litter and surface soil was calculated in kg/ha (Table 6). Mean estimates of initial and final ISN in mg per cylinder, cylinder cross-sectional area, and relative amounts of bare and litter-covered soil surface in each plant community were used to calculate these values.

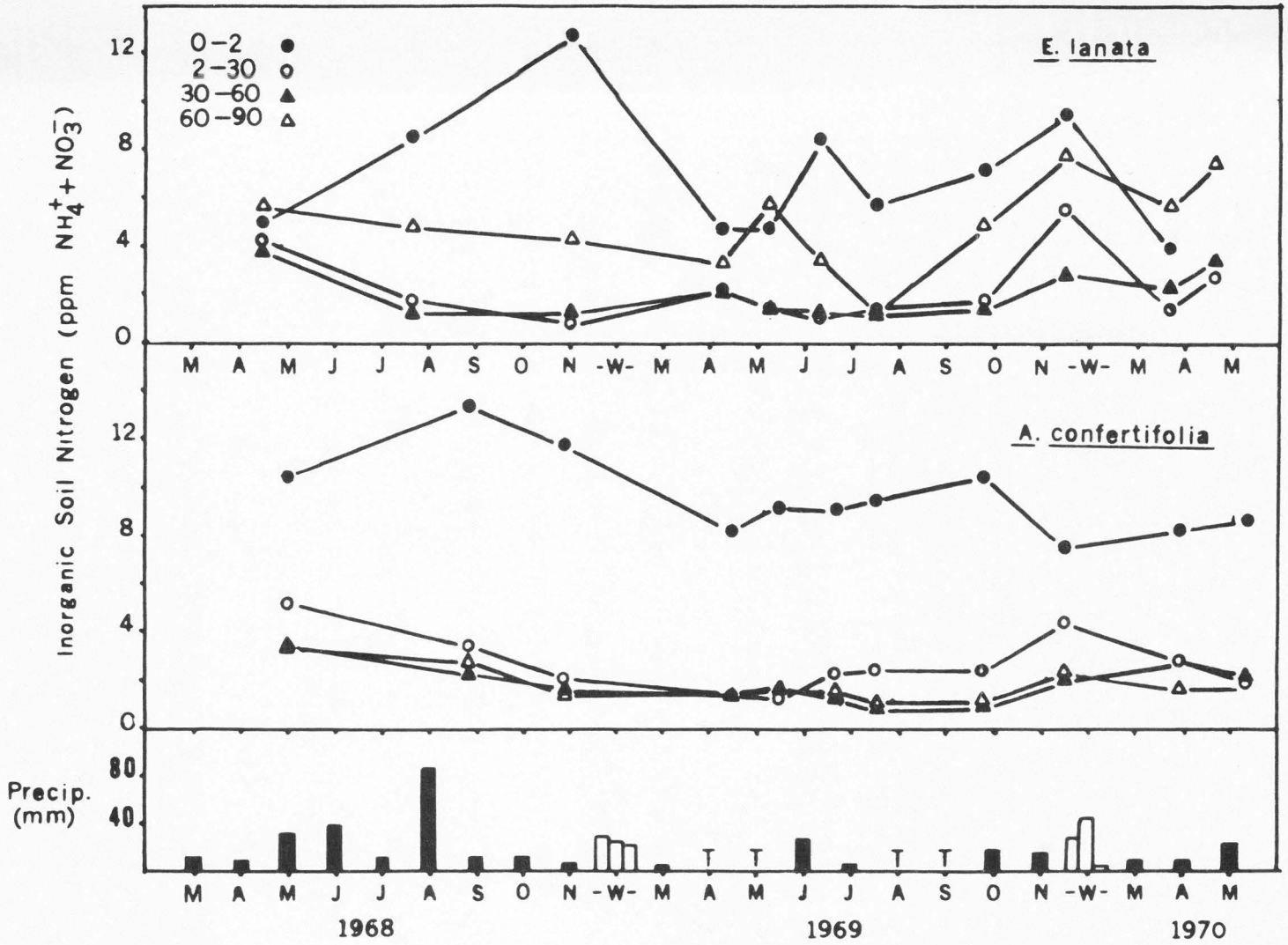
Figure 12 shows the relative ISN distribution in standardized cylinders and compares initial with final ISN distributions under bare and litter-covered soil surfaces in each community.

Results of ISN flux presented in this report were collected from July to November, 1969. Standardized cylinders removed in June of

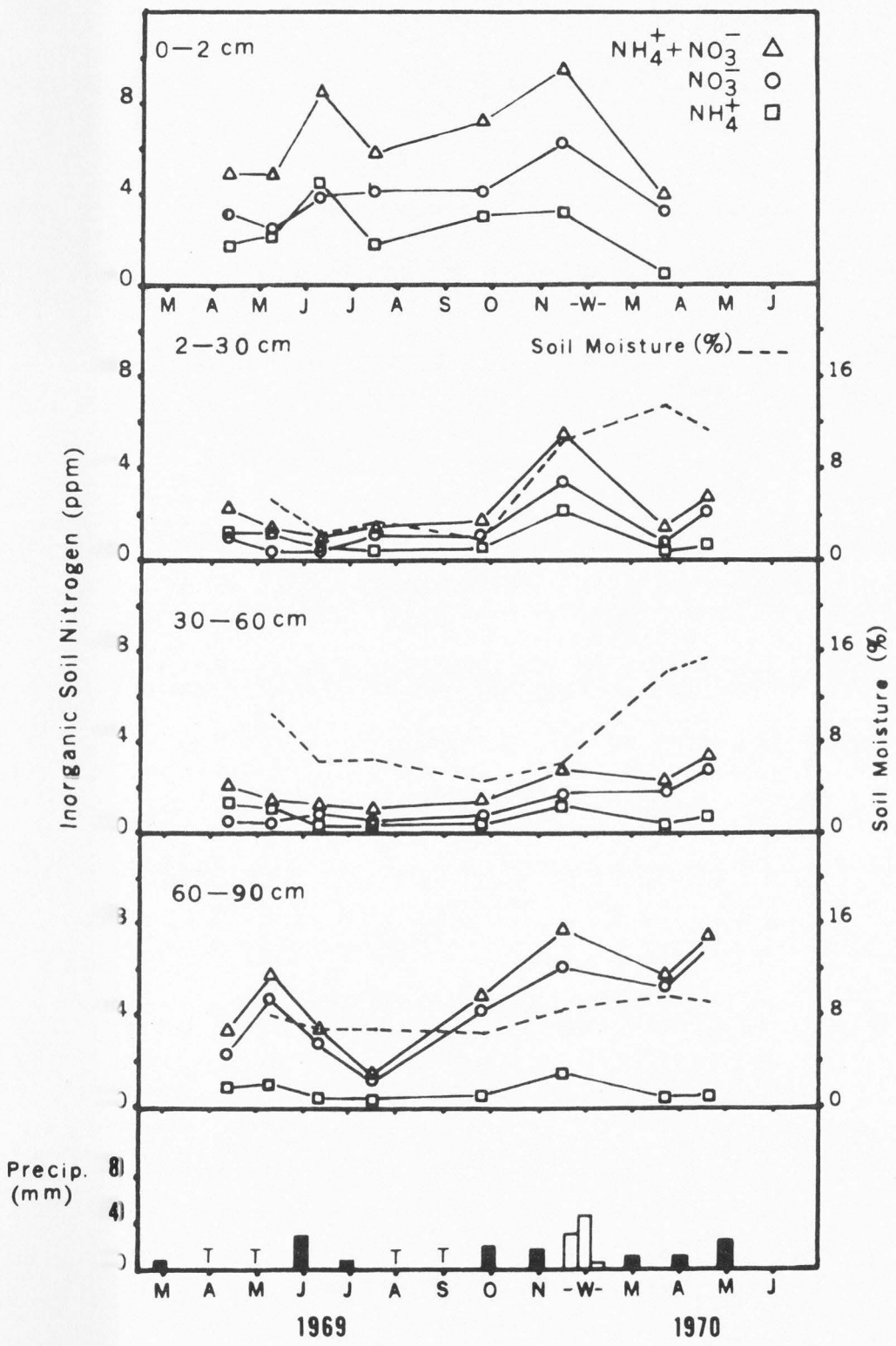
Table 6. Inorganic soil nitrogen flux from surface soil measured by standardized soil cylinders (July to November, 1969).

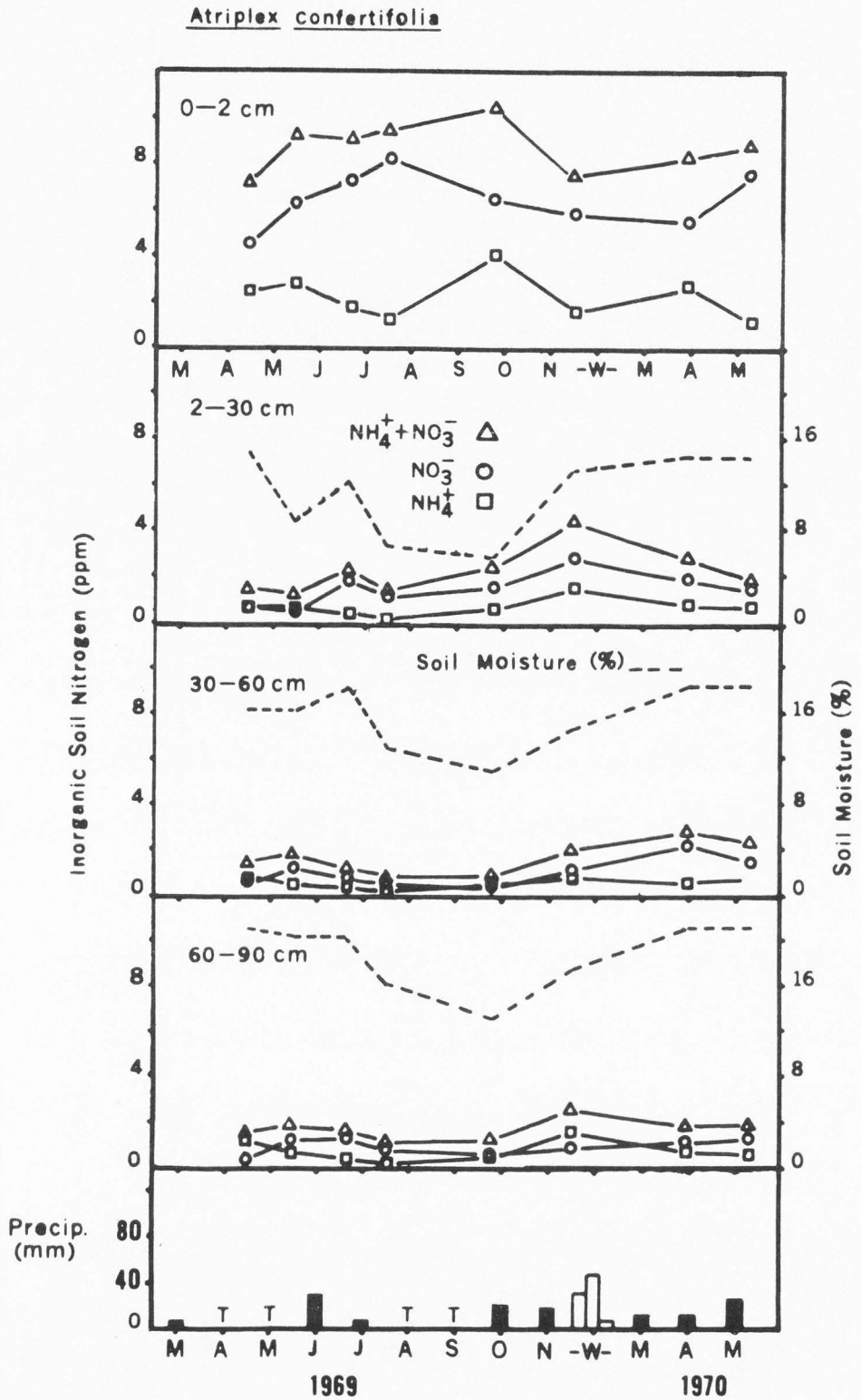
| Soil Surface Type | Initial N Content (mg per Cyl.) | Net Increase per Cylinder (mg per Cyl.) | Net Increase (kg per ha) | |
|---|---|---|---|---|
| *Eurotia* litter | 7.53 | 5.31 | 17.03 | |
| | | | | 13.76* |
| *Eurotia* Bare | 7.53 | 3.53 | 11.34 | |
| *Atriplex* litter | 13.50 | 9.23 | 29.60 | |
| | | | | 23.84* |
| *Atriplex* Bare | 13.50 | 5.49 | 17.61 | |

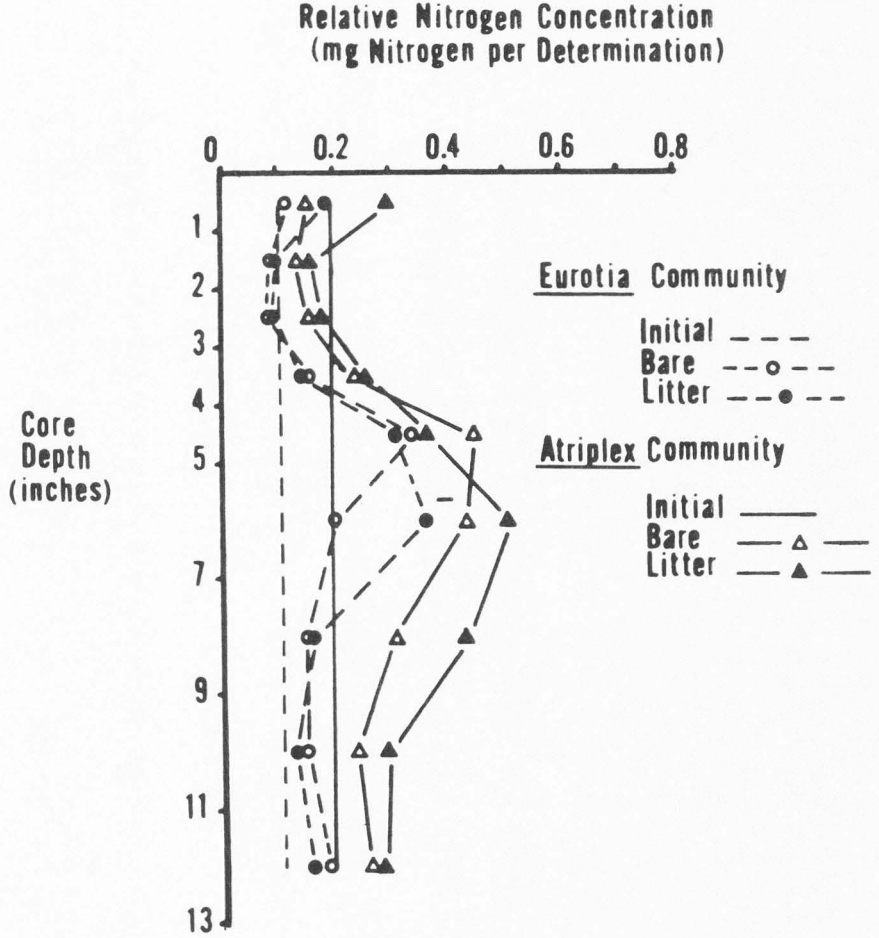
*Flux based upon relative amounts of bare ground and litter-covered soil surface in each plant community.


0–2
2–30
30–60
60–90
E. lanata
A. confertifolia
Inorganic Soil Nitrogen (ppm $NH_4^+ + NO_3^-$)
12
8
4
0
Precip. (mm)
80
40
T
M A M J J A S O N -W- M A M J J A S O N -W- M A M
1968
1969
1970

Eurotia lanata




Atriplex confertifolia
0—2 cm
2—30 cm
30—60 cm
60—90 cm
$NH_4^+ + NO_3^-$
$NO_3^-$
$NH_4^+$
Soil Moisture (%)
Inorganic Soil Nitrogen (ppm)
Soil Moisture (%)
Precip. (mm)
M A M J J A S O N -W- M A M
1969
1970


Relative Nitrogen Concentration
(mg Nitrogen per Determination)
0
0.2
0.4
0.6
0.8
Core
Depth
(inches)
1
2
3
4
5
7
9
11
13
Eurotia Community
Initial
Bare
Litter
Atriplex Community
Initial
Bare
Litter

1970 showed that much of the ISN intercepted had been leached completely through the standardized cylinders rendering them useless for quantative ISN flux comparisons over time. Therefore, information from the June, 1970, collection date is not included in this report.

## Discussion

### Inorganic soil nitrogen dynamics

The soils of salt desert shrub plant communities are annually enriched by nitrogen-containing organic matter from litter fall of shoots and roots and the growth of cryptogams on the soil surface. The organic nitrogen from these sources is gradually made available to higher plants by the following process and transformations. First, organic matter is decomposed and much of the carbon is released as $CO_2$ by numerous bacteria, fungi and actinomycetes. Secondly, organic nitrogen is released as inorganic ammonia after the C:N ratio of organic matter has been reduced and protein becomes a major microbial substrate. Thirdly, ammonia is oxidized to nitrate by very specific chemoautotrophic bacteria at which stage inorganic nitrogen is again available for plant uptake. Higher plants may also utilize ammonia and amino acids in small amounts as a nitrogen source. In general, decomposition of plant residues with high carbon:nitrogen ratios results in a delayed release of inorganic nitrogen due to microbial immobilization of ammonia required for the synthesis of new protein in decomposer organisms (Alexander, 1965).

Much of the surface litter fed into the decomposition cycle of salt desert shrub communities with the exception of Atriplex coarse litter, has a relatively low C:N ratio. According to Alexander

(1965), addition of organic matter containing approximately 1.7 percent (17 mg/gm dry wt.) nitrogen to soil will produce no net change in soil inorganic status while incorporating organic substrates containing more than 1.8 percent nitrogen produces a net release of inorganic nitrogen immediately upon decomposition.

Therefore, if one considers only the rooted part of Eurotia and Atriplex soil profiles, initial decomposition of roots, containing an average of 1.62 and 1.75 percent nitrogen respectively, would probably not depress the ISN status of the soil. Consideration of the high ash content of Eurotia and Atriplex roots makes net ammonia immobilization during initial decomposition even less likely. In Eurotia and Atriplex plants percent ash, determined as mineral weight retained after ignition, is generally greater than 20 percent. The greater part of this ash consists of inert silica ($SiO_2$). Organic matter low in silica usually has an ash content of less than 5 percent (Bazilevich and Rodin, 1968). However, in a given amount of Eurotia or Atriplex plant material silica replaces roughly 15 percent of other organic matter constituents and carbon content is probably decreased in amounts roughly corresponding to 40 percent of increased ash weight. Compared to organic material of low ash content, Eurotia and Atriplex plant remains of equal nitrogen content might contain about 6 percent less carbon. Extension of these theoretical considerations would indicate lower C:N ratios in Eurotia and Atriplex roots than nitrogen content alone would indicate and therefore enhance the likelihood of immediate inorganic nitrogen release during decomposition.

In rooted soil supporting perennial shrubs, decomposing root litter and the sites of nitrogen uptake by living roots are in close

proximity. Root samples often contain live roots growing in and around partially decomposed dead root litter. Thus decomposition and uptake processes in rooted soil have a close spatial relationship and are simultaneously exposed to equivalent soil environments wherever they occur. Therefore, during times of rapid decomposition, rapid ISN uptake is likely to occur provided that ammonia release has not been depressed by microbial immobilization or plant uptake depressed by dormancy.

Conclusions reached by Likens, et al. (1970) indicate that nutrient cycling is closely geared to all components of the ecosystem. Decomposition is adjusted to nutrient uptake and uptake is adjusted to decomposition. This synchrony of decomposition and uptake processes tends to keep ISN concentration low and prevents the accumulation of soluble nitrate subject to loss by leaching or denitrification. Thus the benefits to the overall nitrogen fertility of the plant community provided by close spatial arrangement and synchronous temporal adjustment of decomposition and uptake processes in the rooting zone are obvious.

In parts of the salt desert shrub ecosystem above the rooting zone, including surface soil, litter, and above-ground plant parts, nitrogen transformation pathways are not so temporally related to uptake and are more spatially distinct. Litter fall, decomposition, and mineralization are spatially removed from uptake in the rooting zone. Because of this, inorganic nitrogen can and does accumulate in surface soils of Eurotia and Atriplex plant communities (see Figures 10 and 11) when it is subject to loss from the ecosystem.

The nitrogen concentration in above-ground biomass of Eurotia and Atriplex plant communities is less nitrogen than in roots (Table 1).

Therefore, immobilization of ammonia might be expected to occur in surface soil as new shoot litter is added. However, evidence of immobilization in undisturbed surface soils of salt desert shrub plant communities is lacking. Rather than observing immobilization, one finds the ISN concentration of surface soil to be very responsive to favorable decomposition conditions whenever they occur. Immobilization, if it is occurring, appears to be spatially distinct and mutually exclusive of mineralization and nitrification in other parts of the surface soil. Reasons for this are as follows. Taken collectively, litter has a greater nitrogen concentration (about 1.4 percent) than above-ground biomass (about 1.1-1.2 percent) and in some cases new leaves and twigs (Table 1). This, on the whole, demonstrates a biological concentrating of nitrogen. The concentration of nitrogen might be particularly pronounced in older litter. As deposition occurs, above-ground litter fall is deposited on top of partially decomposed litter fall of previous years so that a vertical stratification and spatial separation usually exists between litter of different ages. Thus it is possible that immobilization of ammonia could occur during initial decomposition in freshly fallen litter at the same time that active mineralization and nitrification is taking place in older litter only a few millimeters below in surface soil.

The existence of relatively high total ISN levels in surface soil throughout the entire year (Figure 9) indicates that net immobilization and mineralization can occur concurrently or that immobilization of ammonia due to addition of fresh litter does not occur. The addition of concentrated nitrogenous compounds through nitrogen fixation by soil surface microflora (Chapter III) could also help to augment the

decomposition of litter and prevent microbial immobilization of ammonia in surface soil.

Physical and biological influences

The concentration and distribution of ISN in the soil profile at a given time is primarily dependent upon rates of decomposition and uptake by plant roots. However, there is a constellation of interacting physical and biological factors which influence these two processes.

The influence of soil moisture on various processes related to inorganic soil nitrogen dynamics are quite substantial. Soil moisture effects on decomposition, mineralization, and nitrification can most easily be observed in surface soil above the rooting zone. Here the effects of infrequent light summer and fall rains, many of which never wet the profile to rooted soil, can be seen when ISN in the surface soil increases to its greatest annual concentration (Figure 9). When heavier precipitation occurs in late fall or over winter, nitrate leaching substantially reduces ISN concentrations in surface soil (Figure 9). Therefore, soil moisture serves to stimulate microbial activity and to redistribute soluble nitrate as it accumulates. As the major part of the soil profile becomes recharged by soil moisture during winter and early spring, further effects of ISN leaching can be observed. Soil moisture may increase and ISN concentration decrease as nitrate from an entire 30 cm sampling increment is leached to lower depths (Figures 10 and 11; winter and spring, 1970).

Within the rooted soil, plant uptake of nitrate is closely related to soil moisture loss due to evapotranspiration. This is best observed by following ISN and soil moisture concentrations during the period of most active plant water use (Figures 10 and 11; May to November).

At various times during the year exchangeable soil ammonia rises abruptly and may even exceed nitrate concentration. Figures 10 and 11 show this to occur during periods of apparently optimum decomposition; i.e., when soil moisture levels are high after winter and early spring recharge or during cool wet periods. At this point reduced soil temperature is also important. This phenomenon can be observed during spring, 1969 in both communities within all sampling depths. At such times it is likely that decomposers are producing ammonia more rapidly than it can be utilized by existing nitrifying organisms. As has been shown in soil perfusion experiments (McLaren, 1969), this situation is rapidly reversed as populations of chemoautotrophic nitrifying bacteria grow in response to increased availability of ammonia substrate.

Under field conditions an abrupt rise in ammonia and lagging nitrification activity can be explained on the basis of fluctuations in microbial populations. Decomposing organisms, which release ammonia as high nitrogen substrates are metabolized, are a diverse group of bacteria, fungi and actinomycetes. These organisms utilize a variety of substrates and collectively are active over a large range of temperatures and soil moisture conditions (Alexander, 1965).

Nitrification, on the other hand, is accomplished by a very specific group of chemoautotrophs which rely solely upon ammonia as an energy source. Therefore, their activity is somewhat restricted and delayed compared to decomposers and rises only in response to substrate production by these decomposers.

Decomposition and mineralization rates appear to be greatest in Atriplex surface soil. Compared to Eurotia surface soil, ISN concen-

trations are usually higher and less variable. This conclusion is also supported by measurements of ISN flux into the rooting zone (Table 6).

Within the main part of the rooted soil in Eurotia and Atriplex communities, the ISN patterns are quite similar over time. However, ISN concentration tends to be greater in the rooted soil of the Eurotia community. This may be expected since the Eurotia community has a greater root biomass. In the Atriplex community soil salinity becomes progressively more limiting to biological activity at greater depths. Total soluble salt concentration below 30 cm depth is commonly 1.5 to 1.7 percent and could account for an osmotic potential of 60-70 bars in the range of available soil moisture. The effects of salinity in Atriplex soils are illustrated by greatly reduced root biomass accumulation (Figure 3) and constantly depressed ISN concentrations (Figures 9, 10, and 11).

Patterns of reduced biological activity with increasing depth in the Eurotia community, are not apparent especially at the 60-90 cm depth. Total soluble salts increase from about 0.4 to 0.50 percent between the 30-60 and 60-90 cm sampling depths respectively. At the same time total nitrogen decreases. Decreased soil nitrogen, Allison and Sterling (1949), and increased soil salinity might be expected to depress decomposition and uptake processes with increasing depth; however, the ISN concentration within the 60-90 cm depth of the Eurotia community is nearly always greater than for the rest of the rooted soil profile. Nitrate concentration at the 60-90 cm depth often exceeds that in surface soil, while ammonia remains characteristically low. These high nitrate concentrations coupled with large annual fluctuations

in nitrate content at this depth cannot be accounted for on the basis of trends in soil salinity, total nitrogen, or soil moisture fluctuations. Concomitant changes in nitrate and soil moisture due to plant uptake are not in evidence at this depth (Figure 10). Calcium carbonate levels at the 60-90 cm depth are high and the C:N ratio of 15.7 for this organic matter is considerably greater than in the upper portions of the soil profile. In peat soil with high C:N ratios and large amounts of active lime, nitrification may be extremely vigorous (Buckman and Brady, 1960), in spite of wide C:N ratios.

Lime concentrations and C:N ratios are parallel in the Eurotia community, but no conclusive evidence exists relating high calcium and C:N ratios with increased nitrification activity. Nitrogen fixation, or upward movement of subsoil moisture with high nitrate content to the 60-80 cm depth, are possible alternative explanations; however, the existence of these phenomena remains in question.

Inorganic soil nitrogen flux

The flux of nitrate from the surface soil into standardized soil cylinders, positioned to intercept moisture and dissolved solutes entering the rooting zone of Eurotia and Atriplex communities, provides a relative measure of net decomposition and nitrification in the plant-soil system above the rooting zone. Assuming that average annual production equals average annual litter fall which in turn is equivalent to average annual decomposition in a stable, moisture-limited, desert plant community, it follows that the average amount of nitrogen in annual above-ground biomass production should be approximately equal to the annual nitrogen flux entering the rooting zone.

Substantial differences in nitrate flux between Eurotia and Atriplex communities were measured (Table 6). However, there were rather large discrepancies between measured nitrate flux and the amount of nitrogen found to be annually accumulated in new growth of above-ground portions of the higher plants. There are a number of possible reasons for the differences and discrepancies observed. A major part of the difference observed between plant communities may be ascribed to the greater above-ground biomass and litter accumulation in the Atriplex community. Assuming comparable rates of litter nitrogen turnover in both communities, the Atriplex litter and surface soil should yield nearly twice the amount of nitrate as produced from the Eurotia litter and surface soil during a given interval of time.

Another part of the nitrate flux differential between plant communities may be associated with the more highly developed, nitrogen-fixing, soil surface microflora of the Atriplex community. The build-up of algae and lichen biomass with very low C:N ratios (Fogg, 1947; Fuller, et al., 1960) and the excretion of nitrogenous metabolites (Fogg, 1947; Mayland and McIntosh, 1966) may be augmenting decomposition processes. The results of nitrogen fixation experiments (see Chapter III) indicate that the Atriplex surface soil would receive the greatest benefit to decomposition which is consistent with the experimental results.

Differences in nitrate flux between communities were observed under apparently bare soil surface. Here litter accumulates in soil cracks, but in lesser amounts than in the immediate vicinity of plants. These bare areas are also the areas of greatest soil surface micro-flora development and thus might be expected to indicate the differ-

ential input from cryptogams in the two communities. This difference is about 6 kg/ha (Table 6), a figure which agrees more closely with the nitrogen fixation for 58 days of incubation for Atco-H soil crusts (Table 5).

Nitrate flux exceeded the amount of nitrogen in new growth (Tables 1 and 6). Microbial release of nitrate from soil within the standardized soil cylinder may account for part of this difference. However, the contribution from intracylinder nitrification was not great enough to mask the difference between cylinders placed under bare and litter-covered soil surface. A more plausible explanation for this discrepancy may be the fact that surface soil nitrification was unavoidably disturbed during standardized cylinder installation. The increased rate of decomposition and mineralization of nitrogen in disturbed soil compared to undisturbed soil of the same type is well known (Alexander, 1965; Tisdale and Nelson, 1966). There are also portions of above-ground production and subsequent litter fall unaccounted for by experimental methods used; i.e., fall of leaves grown in early spring before summer sampling and new growth increments on older stems and associated nitrogen. These, like all other above-ground plant materials, are subject to decomposition and can account for a part of the discrepancy observed between nitrogen in annual production and nitrogen in ISN flux.

Nitrate flux for the period November through June of 1969-70 remains unevaluated. Nitrate flux during November to March of this period was probably negligible due to frozen soil conditions. However, decomposition and nitrate flux from surface soil during the spring of 1970 was probably appreciable (see Tables 10 and 11), especially in

the Eurotia community which showed the greatest loss of nitrate from surface soil via leaching. Thus nitrate leaching during the winter and spring period of 1970 would have further accentuated the discrepancy between nitrogen in annual production and total nitrate flux.

# CHAPTER V

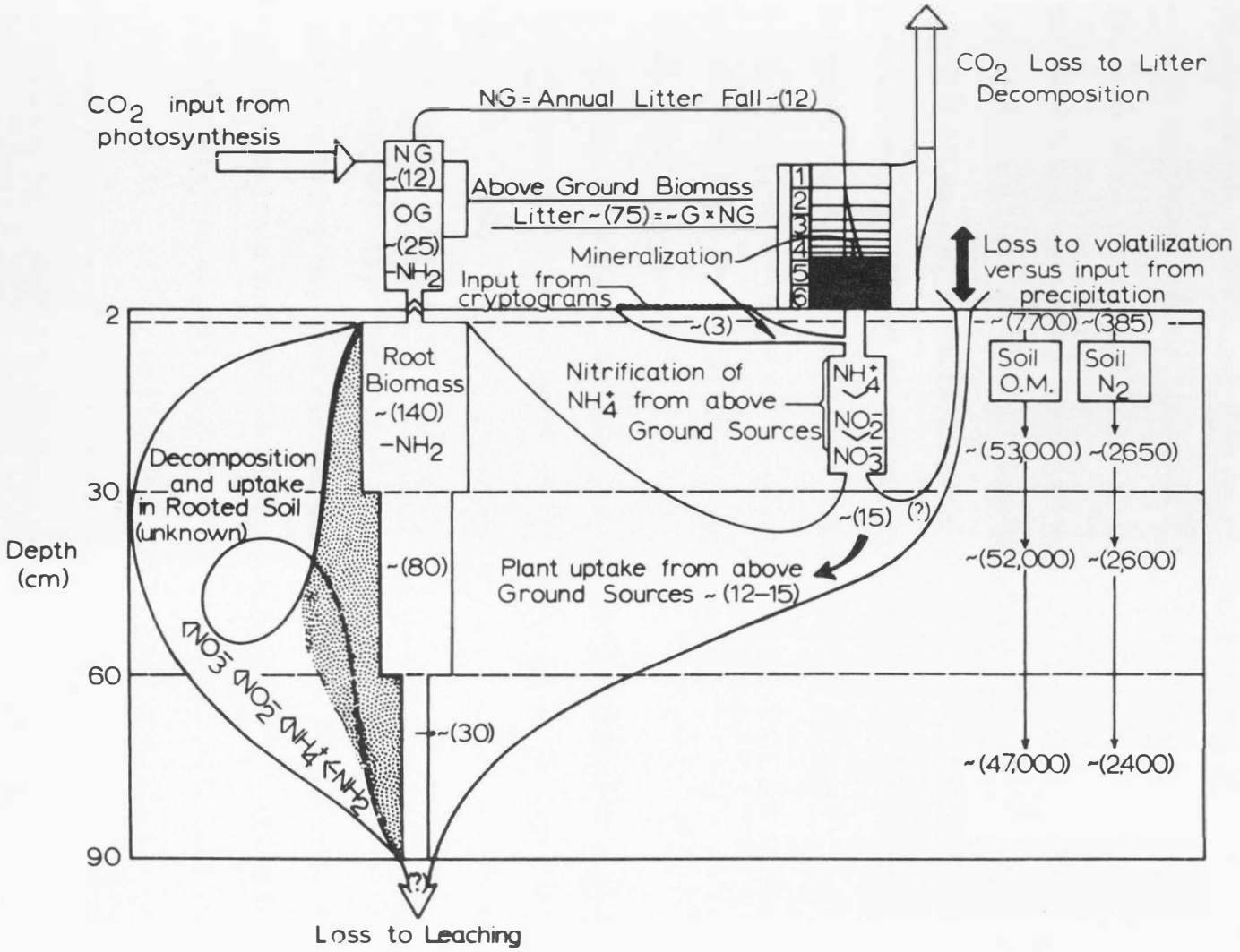
## INTEGRATION AND CONCLUSIONS

The nitrogen budget of a composite northern salt desert shrub ecosystem is illustrated in diagramatic form in Figure 13. This figure combines the essential characteristics of both Eurotia and Atriplex communities into a conceptual model. The approximate weight of nitrogen-containing biomass, litter, and organic matter compartments evaluated in the study are roughly proportional to the area occupied by each in the diagram. Approximate amounts of nitrogen contained in various compartments of the system are represented by numbers in parentheses while estimated rates of nitrogen transfer from one component to another are designated by number and appropriate directional arrows. Unknown rates of nitrogen transfer are indicated by a question mark in parentheses.

It is essential, for the purposes of interpretation, that the salt desert shrub ecosystem represented in Figure 13 is in a steady state condition. There is ample evidence that plant communities in the study area have undergone a long developmental period and achieved a near steady state condition. The area is known to have been above the level of Lake Bonneville since water receded from the Stansbury level beaches about 13,500 years ago (Eardley, Grovetsky, and Marsell, 1957), and has experienced roughly the same climatic regime since about 8,000 B.P. (Bright, 1966; Harper and Alder, 1971).

As the lake waters receded, lake-bottom sediments and extensive littoral vegetation at the margins of the Pleistocene lake may have

Figure 13. Diagramatic representation of a composite salt desert shrub ecosystem of western Utah. The diagram illustrates relative sizes of organic matter and nitrogen compartments, rates of nitrogen cycling, and nitrogen transformation processes in the ecosystem.


$CO_2$ input from photosynthesis
NG = Annual Litter Fall ~(12)
NG ~(12)
OG ~(25)
$NH_2$
Above Ground Biomass Litter ~(75) = ~G × NG
$CO_2$ Loss to Litter Decomposition
Mineralization
Input from cryptograms
Loss to volatilization versus input from precipitation
~(3)
~(7,700) ~(385)
Soil O.M.
Soil $N_2$
Root Biomass ~(140) $-NH_2$
Nitrification of $NH_4^+$ from above Ground Sources
$NH_4^+$
$NO_2^-$
$NO_3^-$
~(53,000) ~(2650)
Decomposition and uptake in Rooted Soil (unknown)
~(15) (?)
~(80)
Plant uptake from above Ground Sources ~ (12–15)
~(52,000) ~(2600)
$\Gamma NO_3^- \Gamma NO_2^- \Gamma NH_4^+ \Gamma NH_2$
~(30)
~(47,000) ~(2400)
Depth (cm)
2
30
60
90
(?)
Loss to Leaching

endowed the desert plant communities which subsequently developed with an ample pool or organic nitrogen. With a pool of organically incorporated nutrients already available, the establishment of desert vegetation was probably not limited by nitrogen and could have developed rapidly into plant communities much like those present today. During the time since initial development, nitrogen in amounts adequate to maintain these vegetation types has probably been supplied by nitrogen fixation. As long as relatively stable vegetation-climate equilibrium exists, nitrogen fixation probably serves a maintenance role by replacing losses to volatilization, denitrification, leaching, natural erosion, and grazing. In a mature and undisturbed ecosystem these losses are individually small, but collectively may cause a significant drain on ecosystem nitrogen reserves for which nitrogen fixation must compensate.

Plant productivity in desert ecosystems is limited by moisture. Thus drier conditions, as occur in the course of small climatic fluctuation, are likely to cause a reduction in plant growth and reduce vegetal cover. Concomitant nitrogen loss from the ecosystem would also occur under these periods of severe moisture limitation. Nitrogen fixation activity would be reduced while nitrogen losses to erosion from bared surface soil and volatilization would be accelerated.

The nitrogen content of various plant parts, litter, and soil organic matter does not vary substantially. For instance the carbon: nitrogen ratio of soil organic matter varies little from a mean of 12.3 (Table 3). Similar relationships exist between nitrogen and carbon in plant parts and litter as well. Thus when new biomass production is limited by moisture, biomass, litter, and soil organic matter and the associated nitrogen pool must fall to a lower equilibrium level.

Conversely a more moist climatic regime would allow a larger biomass and nitrogen pool to develop. Improved moisture conditions would stimulate plant growth, increase vegetal cover thereby reducing nitrogen loss to erosion, reduce volatilization loss, and stimulate increased nitrogen fixation. In general, greater competition among ecosystem components for inorganic soil nitrogen would reduce overall losses relative to nitrogen inputs and allow a larger biomass and associated nitrogen pool to accumulate.

As shown in Figure 13, a relatively small amount of nitrogen is annually cycled into new leaf and twig growth. The average for Eurotia and Atriplex communities is about 11 kg/ha/yr. If new growth increments on old stems were considered, the estimate would rise only about one kg/ha/yr. This estimate is derived by assuming the age class distribution of these communities is relatively constant and that the mean age of perennial shrubs is at least numerically equal to the number of kg/ha of nitrogen present in old stems.

Assuming that the ecosystem represented in Figure 13 is mature, moisture-limited, and in relatively undisturbed condition, average annual above-ground productivity and associated nitrogen should equal average annual litter fall. Litter, including animal feces is not immediately decomposed. Litter accumulates and remains for several years. However, the annual decomposition and nitrogen mineralization of the collective litter accumulation of many years must equal the annual litter fall. In salt desert shrub communities the total accumulation of litter and associated nitrogen is equivalent to the average input of six to seven years of annual shoot productivity; however, litter decomposition residues of much greater age may be found

in the litter layer. By the time litter is finally reduced to humus in surface soil, the mean residence time for carbon may exceed 100 years. Dahlman and Kucera (1968) estimated the time required for organic matter in the $A_1$ horizon of a prairie soil to reach 99 percent equilibrium to be 110 years. However, most of the nitrogen mineralized from plant litter is derived from increments of much younger age. This plant litter, whether from root or shoot sources, is the most readily available source of inorganic soil nitrogen in the ecosystem. Based upon nitrogen added by annual litter fall, estimated net annual mineralization of ammonia from above-ground litter is about 10-12 kg/ha.

Ammonia released to surface soil by decomposition is retained by the cation exchange complex of surface soil while being oxidized to nitrate by nitrifying bacteria. Nitrifying activity in surface soil of salt desert shrub communities is relatively vigorous and with the exception of certain decomposition conditions, discussed in Chapter IV, maintains ammonia concentrations at less than 3-4 ppm. Maintenance of low ammonia concentrations in surface soil is important, since ammonia allowed to accumulate in a hot and drying surface soil is subject to substantial volatilization. Figures 10 and 11 for Eurotia and Atriplex communities indicate that peaks in surface soil ammonia concentrations are usually followed by comparably higher nitrate and reduced ammonia concentrations in the absence of significant leaching, which indicates that volatilization is probably minimal in spite of high surface soil temperature and pH (Figures 10 and 11). Junge (1958) reported that atmospheric ammonia is largely derived from ammonia volatilization in alkaline soils; however, the nitrogen in atmospheric ammonia is returned in precipitation as nitrate after photochemical

oxidation. Since the study area is in the center of an area of alkaline soils extending several hundred miles in all directions, nitrogen input from precipitation may well equal losses to volatilization. Dew fall might also serve to return ammonia volatilized in the vicinity of the plant community.

The rooted soil of salt desert shrub communities represents a relatively closed system with respect to nitrogen uptake and decomposition processes. Although annual root biomass production and inorganic nitrogen uptake could not be evaluated by the experimental methods used in this investigation, indications are that losses of nitrogen from rooted soil are small. Ammonia nitrogen concentrations in rooted soil remain consistently low and vary less than nitrate concentrations. Thus losses to volatilization are considered to be small. Furthermore, infiltrating soil moisture, containing soluble nitrates, seldom penetrates deeper than 90 cm. As a result, nitrate is probably not carried beyond the rooting zone of plants and lost to the ecosystem by leaching.

A critical comparison of the nitrogen budgets of Eurotia and Atriplex communities, reveals them to be ecologically equivalent in most respects. For example, total plant biomass is roughly equivalent. Above ground productivity and nitrogen cycling rates are comparable, especially if differences in growth habit and biomass of above-ground plant parts is taken into account.

The principal difference in the two plant communities appears to be in nitrogen-fixation potential. Experimental results indicate the Eurotia community to lack a nitrogen-fixing flora (Chapter III), which may help to explain why Eurotia lanata stands are giving way to

Atriplex confertifolia wherever adjacent stands of the two shrubs are subjected to severe environmental perterbation such as excessive grazing. Severe trampling during past domestic use among small-statured Eurotia plants growing in sandy soils may have disrupted the nitrogen-fixing soil surface flora to the extent that present fixation levels are below the level of detection. Thus it is not unlikely that under a more favorable history of domestic use both plant communities would exhibit comparable nitrogen fixation.

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# APPENDIX

Table 7. Estimates of total above-ground plant biomass and nitrogen in E. lanata and A. confertifolia plant communities for the years 1968-70.

| Year | Item | Eurotia lanata Biomass kg/ha | Eurotia lanata mg N/gm dry wt. | Eurotia lanata Kg N /ha | Atriplex confertifolia Biomass kg/ha | Atriplex confertifolia mg N/gm dry wt. | Atriplex confertifolia Kg N /ha |
|---|---|---|---|---|---|---|---|
| 1968 | Shoots | -2220- | 10.64 | -23.6- | -3770- | 11.65 | -43.9- |
| | New Growth* | 830 | 10.95 | 9.1 | 780 | 12.81 | 10.0 |
| | Old Growth* | 1390 | 10.60 | 14.7 | 2990 | 9.55 | 28.6 |
| | Fine Litter | -3810- | 13.51 | -51.5- | -4260- | 13.24 | -56.4- |
| | Coarse Litter | ---- | ----- | ---- | -4460- | 9.83 | -43.8- |
| | 1968 Totals | -6030- | | -75.1- | -12,490- | | -144.1- |
| 1969 | Shoots | -2300- | 12.89 | -29.7- | -4790- | 11.43 | -54.7- |
| | New Growth | 500 | 14.98 | 7.5 | 610 | 17.77 | 10.8 |
| | Old Growth | 1800 | 11.85 | 21.3 | 4180 | 10.27 | 42.9 |
| | Fine Litter | -3550- | 15.40 | -54.7- | -3800- | 13.29 | -50.5- |
| | Coarse Litter | ---- | ----- | ---- | -4790- | 10.88 | -52.1- |
| | 1969 Totals | -5850- | | -84.4- | -13,380- | | -157.3- |
| 1970 | Shoots | -2720- | 12.16 | -33.1- | -3940- | 10.82 | -42.6- |
| | New Growth | 760 | 12.62 | 9.6 | 1130 | 13.27 | 15.0 |
| | Old Growth | 1960 | 10.79 | 21.2 | 2810 | 10.00 | 28.1 |
| | Fine Litter | -4650- | 13.52 | -62.9- | -4030-* | 10.59* | -53.5-* |
| | Coarse Litter | ---- | ----- | ---- | -4130- | 9.08 | -37.5- |
| | 1970 Totals | -7370- | | -96.0- | -12,100- | | -133.6- |

*Mean estimate for the years 1968-69 only

Table 8. Estimates of total below-ground plant biomass and nitrogen in E. lanata and A. confertifolia plant communities for the years 1968-70.

| | | Eurotia lanata | | | Atriplex confertifolia | | |
|---|---|---|---|---|---|---|---|
| Year | Depth | Biomass kg/ha | mg N/gm dry wt. | Kg N /ha | Biomass kg/ha | mg N/gm dry wt. | Kg N /ha |
| 1968 | 2-30 | 7890 | 16.53 | 130 | 9330 | 16.38 | 153 |
| | 30-60 | 5880 | 16.07 | 94 | 2560 | 18.54 | 47 |
| | 60-90 | 1180 | 17.98 | 21 | 600 | 19.87 | 12 |
| 1968 Totals | | -14,950- | | -245- | -12,490- | | -212- |
| 1969 | 2-30 | 4820 | 14.39 | 69 | 7480 | 15.83 | 118 |
| | 30-60 | 6370 | 14.37 | 92 | 2610 | 17.74 | 46 |
| | 60-90 | 1700 | 17.64 | 30 | 470 | 19.55 | 9 |
| 1969 Totals | | -12,890- | | -191- | -10,560- | | -173- |
| 1970 | 2-30 | 8910 | 16.95 | 151 | 11,550 | 17.66 | 204 |
| | 30-60 | 7800 | 16.61 | 130 | 3600 | 16.86 | 61 |
| | 60-90 | 3660 | 18.23 | 67 | 1200 | 20.00 | 24 |
| 1970 Totals | | -20,370- | | -348- | -16,350- | | -289- |

Table 8a. Sample sizes, means, and standard deviations for biomass sampling in Eurotia and Atriplex plant communities for the years 1968-70. Units of measurement are: (1) $g/m^2$ for above-ground biomass, fine litter, and coarse litter, and (2) g/core for root cores 8.30 cm in diameter and 90 cm deep. Old growth:new growth ratios are dimensionless.

| | | | Eurotia lanata | | Atriplex confertifolia | |
|---|---|---|---|---|---|---|
| Year | Item | n | $\bar{x}$ | $S\bar{x}$ | $\bar{x}$ | $S\bar{x}$ |
| 1968 | Above-ground biomass | 18 | 222 | 13.20 | 377 | 25.94 |
| | OG/NG ratio | 40 | 1.68 | 0.27 | 3.85 | 0.31 |
| | Fine litter | 18 | 381 | 16.40 | 426 | 20.50 |
| | Coarse litter | 18 | --- | ----- | 446 | 22.20 |
| | Below-ground biomass | 35 | 8.08 | 0.47 | 6.75 | 0.38 |
| 1969 | Above-ground biomass | 18 | 230 | 13.30 | 479 | 24.60 |
| | OG/NG ratio | 40 | 3.53 | 0.22 | 6.85 | 0.44 |
| | Fine litter | 18 | 355 | 19.40 | 380 | 15.90 |
| | Coarse litter | 18 | --- | ----- | 479 | 20.90 |
| | Below-ground biomass | 35 | 6.97 | 0.33 | 5.71 | 0.30 |
| 1970 | Above-ground biomass | 18 | 272 | 16.25 | 395 | 25.60 |
| | OG/NG ratio | 40 | 2.59 | 0.14 | 2.50 | 0.26 |
| | Fine litter | 18 | 465 | 47.80 | --- | ---- |
| | Coarse litter | 18 | --- | ----- | 413 | 18.80 |
| | Below-ground biomass | 35 | 11.01 | 0.54 | 8.84 | 0.47 |

Table 9. Analysis of variance for above-ground biomass in Eurotia lanata and Atriplex confertifolia plant communities during the years 1968-70.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Years (y) | 2 | 27,499.51* |
| Communities (c) | 1 | 832,484.50** |
| y x c | 2 | 39,247.12** |
| Error | 102 | 7,745.07 |
| Total | 107 | 16,410.98 |

*Significant at the .05 level of probability
**Significant at the .01 level of probability

Table 10. Analysis of variance for old growth:new growth ratios of above-ground biomass in Eurotia lanata and Atriplex confertifolia plant communities during the years 1968-70.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Plant Communities (c) | 1 | 191.07** |
| Years (y) | 2 | 175.71** |
| c x y | 2 | 58.66** |
| Error | 234 | 2.83 |
| Total | 239 | 5.95 |

**Significant at the .01 level of probability

Table 11. Analysis of variance for litter of fine composition in Eurotia lanata and Atriplex confertifolia plant communities during the years 1968-70.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Years (y) | 2 | 16,580.36 |
| Communities (c) | 1 | 50,052.08* |
| y x c | 2 | 167,116.70** |
| Error | 102 | 8,971.79 |
| Total | 107 | 12,453.92 |

*Significant at the .05 level of probability
**Significant at the .01 level of probability

Table 12. Analysis of variance for Atriplex coarse litter collected during the years 1968-70.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Years | 2 | 19,536.72 |
| Error | 51 | 7,272.11 |
| Total | 53 | 7,734.93 |

Table 13. Analysis of variance for below-ground biomass (roots and root litter) in Eurotia lanata and Atriplex confertifolia plant communities during the years 1968-70.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Years (y) | 2 | 792.058.20** |
| Communities (c) | 1 | 443,902.70** |
| Depth (d) | 2 | 7,233,827.00** |
| y x c | 2 | 15,077.86 |
| y x d | 4 | 172,764.10** |
| c x d | 2 | 1,409.924.00** |
| y x c x d | 4 | 33,481.88 |
| Error | 612 | 15,881.97 |
| Total | 629 | 47,520.55 |

**Significant at the .01 level of probability

Table 14. Analysis of variance for composite samples of Atriplex soil surface with heavy and light lichen cover incubated to evaluate nitrogen fixation potential.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Surface Type (t) | 1 | 37.675** |
| Incubation Treatment (i) | 2 | 5.092** |
| t x i | 2 | 0.573* |
| Error | 42 | 0.146 |
| Determinations | 48 | 0.004 |
| Total | 95 | 0.583 |

*Significant at the .05 level of probability
**Significant at the .01 level of probability

Table 15. Analysis of variance for composite samples of Eurotia soil surface organisms incubated to evaluate nitrogen fixation potential.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Incubation Treatment | 2 | 0.047 |
| Error | 15 | 0.052 |
| Determinations | 18 | 0.001 |
| Total | 35 | 0.025 |

Table 16. Analysis of variance for total inorganic soil nitrogen ($NH_3$+$NO_3^-$) in Eurotia lanata and Atriplex confertifolia plant communities at three depths and eleven sampling dates during the years 1968-70.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Communities (c) | 1 | 129,108.10** |
| Depths (d) | 2 | 99,648.66** |
| c x d | 2 | 162,685.80** |
| Error (a) | 54 | 1,569.64 |
| Sampling Dates (s) | 10 | 47,622.07** |
| Error (b) | 90 | 2,125.61 |
| c x s | 10 | 9,549.31** |
| d x s | 20 | 5,491.35** |
| c x d x s | 20 | 3,459.92** |
| Error (c) | 540 | 1,399.95 |
| Total | 659 | 3,407.05 |

**Significant at the .01 level of probability

Table 17. Analysis of variance for inorganic soil nitrogen ($NO_3^-$) in Eurotia lanata and Atriplex confertifolia plant communities at three depths and eleven sampling dates during the years 1968-70.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Communities (c) | 1 | 137,059.30** |
| Depths (d) | 2 | 98,510.62** |
| c x d | 2 | 172,933.40** |
| Error (a) | 54 | 1,556.82 |
| Sampling dates (s) | 10 | 18,538.08** |
| Error (b) | 90 | 1,824.19 |
| c x s | 10 | 7,754.38** |
| d x s | 20 | 3,859.16** |
| c x d x s | 20 | 3,170.04** |
| Error (c) | 540 | 1,274.24 |
| Total | 659 | 2,815.80 |

**Significant at the .01 level of probability

Table 18. Analysis of variance for inorganic soil nitrogen ($NH_3$) in Eurotia lanata and Atriplex confertifolia plant communities at three depths and eleven sampling dates during the years 1968-70.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Communities (c) | 1 | 118,79 |
| Depths (d) | 2 | 1,606.51** |
| c x d | 2 | 243.84 |
| Error (a) | 54 | 174.13 |
| Sampling Dates (s) | 10 | 17,654.17** |
| Error (b) | 90 | 197.92 |
| c x s | 10 | 1,361.73** |
| d x s | 20 | 481.01** |
| c x d x s | 20 | 160.25 |
| Error (c) | 540 | 128.47 |
| Total | 659 | 433.36 |

**Significant at the .01 level of probability

Table 19. Analysis of variance for standardized soil cylinders installed under bare and litter-covered soil surfaces in *Eurotia lanata* and *Atriplex confertifolia* plant communities from July 1 to November 15, 1969.

| Sources of variation | d.f. | Mean Squares |
|---|---|---|
| Communities (c) | 1 | 69.064** |
| Soil Surface Type (t) | 1 | 60,717** |
| c x t | 1 | 7.707 |
| Error | 28 | 3.929 |
| Total | 31 | 7.984 |

**Significant at the .01 level of probability

# VITA

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